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No. 309

**CRETACEOUS AND TERTIARY CIDAROIDA
(ECHINODERMATA: ECHINOIDEA) OF THE
CARIBBEAN AREA**

By

BERTHA M. CUTRESS

1980

Paleontological Research Institution
Ithaca, New York 14850 U. S. A.

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CRETACEOUS AND TERTIARY CIDAROIDA (ECHINODERMATA: ECHINOIDEA) OF THE CARIBBEAN AREA*

By

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Department of Marine Sciences
University of Puerto Rico at Mayagüez

ABSTRACT

Careful examination of previously unreported collections of Caribbean area cidaroid specimens (mostly made by R. H. Palmer and P. J. Bermúdez in Cuba between 1929 and 1946) and of most of the specimens previously recorded in publications, shows that the Order Cidaroida was well represented in the Caribbean during the Cretaceous and Tertiary periods. The specimens, most now deposited in United States museums, have been assigned to 12 genera (three new: *Palmerius*, *Fellius*, *Prophyllacanthus*) and 24 species (four indeterminate, seven new: *Cidaris bermudezi*, *Calocidaris palmeri*, *Tretocidaris anguillensis*, *Palmerius roberti*, *Prionocidaris katherinae*, *Prophyllacanthus eocenicus*, *Tylocidaris bermudezi*). Evolutionary trends, faunal relationships, possible dispersal routes, introductions and extinctions, faunal affinities, and stratigraphic markers, as pertinent to Caribbean cidaroids, are discussed.

INTRODUCTION

This study was initiated some years ago under the aegis of a petroleum company. They needed an illustrated manual of fossil echinoid spines that could be used to identify material from well cores; it was hoped that the spines would prove useful as stratigraphic markers. It became obvious as work proceeded that consideration of test material was necessary if the spine identifications were to have validity. Because most of the available fossil echinoid spines belong to the Order Cidaroida and because non-cidaroid tests are receiving ample attention from others, the scope of my study was narrowed to the Cidaroida.

Most of the specimens considered here were found in museum collections. A large proportion of these had been collected by Dr. Robert H. Palmer during the 17 years (1929 to 1946) that he and his wife, Dr. Dorothy K. Palmer, collected in Cuba. During the latter part of this period, several monographs were being prepared by R. H. Palmer on the echinoids in this collection, and some of the labels with the specimens bear manuscript names. However, the papers

*Contribution, Department of Marine Sciences, University of Puerto Rico, Mayagüez, P. R. 00708.

were not published before his death. The Palmer cidaroid specimens are now widely scattered in the United States. Most are in the collections of the Paleontological Research Institution, Ithaca, New York. Others are in the California Academy of Sciences, San Francisco (transferred there in 1977 from the Department of Geology, Stanford University); Museum of Paleontology, University of California at Berkeley; Museum of Comparative Zoology, Harvard University; and the Academy of Natural Sciences of Philadelphia.

Additional specimens, from Cuba and the Dominican Republic, were part of the large personal collection of Dr. Pedro J. Bermúdez (Dirección de Geología, Ministerio de Minas e Hidrocarburos, Caracas, Venezuela) and were kindly made available without restriction for the duration of this study. These specimens are now deposited in the Paleontological Research Institution, Ithaca, New York. Seven other Cuban specimens, all belonging to one species and collected by F. W. Penney for the U.S. Geological Survey, are in collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Some of the Puerto Rican specimens were collected by Dr. C. A. Reeds and Mr. Prentice B. Hill, during an expedition sponsored jointly by the New York Academy of Sciences, the American Museum of Natural History, and the Puerto Rican government; these are now in the American Museum of Natural History. Other specimens, now in collections of the [U. S.] National Museum of Natural History, were collected by Dr. T. W. Vaughan, and Dr. C. W. Cooke and his assistant, Mr. A. D. Watt, for the U. S. Geological Survey, and by Dr. W. A. Gordon and Dr. H. R. Bergquist. A small number of the Puerto Rican specimens, some collected by Prof. Edgardo Ortiz-Corps (Department of Biology, University of Puerto Rico Regional College, Humacao, P.R.) and a few personally collected, are now in the Paleontological Research Institution, Ithaca, N.Y.

Some of the Jamaican specimens included in this study are in the Museum of Comparative Zoology, Harvard University, and were collected by Drs. B. W. Arnold and R. T. Hill. Others were collected by Dr. Norman D. Sohl and others of the U.S. Geological Survey and are deposited in the [U.S.] National Museum of Natural History.

Specimens from Anguilla and St. Bartholomew that were collected by Prof. P. T. Cleve and that later became part of the R. J. L. Guppy collection, are now in the [U.S.] National Museum of Natural History, as are specimens from Antigua collected by W. R. Forest and several specimens from Trinidad and the Dominican Republic collected by Drs. T. W. Vaughan, C. W. Cooke and D. D. Condit of the U.S. Geological Survey.

Prof. N. E. Weisbord made available several specimens he had collected in Venezuela; some are now at the Paleontological Research Institution and others are in the collections of the Department of Geology, Florida State University.

The total, 167 test and 3628 radiole specimens, whole or fragmented, were carefully measured and photographed. These specimens are here assigned to 24 species (seven new, four indeterminate) in 12 genera (three new) and two indeterminate genera. Of the 12 previously known species, seven are new combinations. A list of the Caribbean Recent and fossil cidaroids, the latter with geological distributions, appears in Table 16.

In this study, generic and specific assignment of the Caribbean fossil cidaroid specimens followed and depended to a considerable extent on my morphometric measurements of Recent species. The Recent species studied were not only from the Caribbean area but also from the eastern Atlantic, Mediterranean and Indo-Pacific. Many of these species appear to be closely related to some of the Caribbean fossils. Summaries of these data are recorded in the Appendix.

ABBREVIATIONS OF REPOSITORIES

Names of museums or museum collections are abbreviated as follows:

- AMNH —American Museum of Natural History, New York, NY, USA
- ANSP —Academy of Natural Sciences of Philadelphia, Philadelphia, PA, USA
- BM —British Museum (Natural History), London, England
- CASGTC —California Academy of Sciences, Geological Type Collection, San Francisco, CA, USA

GSI	—Geological Survey of India, New Delhi, India
HM	—Hunterian Museum, University of Glasgow, Glasgow, Scotland
LSJU	—Stanford University, Regular Collection* (California Academy of Sciences, San Francisco, CA, USA)
MCZ	—Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
PRI	—Paleontological Research Institution, Ithaca, NY, USA
Sedgwick	—Sedgwick Museum, University of Cambridge, Cambridge, England
SUPTC	—Stanford University, Paleontological Type Collection* (California Academy of Sciences, San Francisco, CA, USA)
UCMP	—Museum of Paleontology, University of California, Berkeley, CA, USA
USNM	—[U.S.] National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

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I deeply appreciate help from many sources during the long course of this study.

Grants from the Jersey (now Exxon) Production Research Company, National Science Foundation (G-15902), and the University of Puerto Rico, Mayagüez campus (69-24 and 70-78) provided part of equipment and materials, and supported travel to museums. The Smithsonian Institution administered the first two grants and provided working space and access to their collections and Central Library for several years, during which time many employees gave their help; very special thanks are due Dr. Fenner A. Chace, Jr., Dept. of Invertebrate Zoology, and Dr. Porter M. Kier, Department of Paleobiology. The largest part of the work was done while I was employed by the Department of Marine Sciences, University of Puerto Rico, Mayagüez, where facilities, equipment and many of the supplies were provided.

*The Stanford specimens have been transferred to the California Academy of Sciences, but retain SUPTC and LSJU catalogue numbers.

I am grateful to the following who arranged working space, access to collections and libraries and loan of specimens during my visits to their museums: Dr. Katherine V. W. Palmer, Director Emeritus, Paleontological Research Institution; Dr. David L. Pawson, Miss Maureen Downey, Dr. Porter M. Kier, and Librarian Jack Marquardt, [U.S.] National Museum of Natural History, Smithsonian Institution; Dr. Bernard Kummel, the late Dr. Elizabeth Deichmann, Dr. H. B. Fell, and Miss Charlene D. Long, Museum of Comparative Zoology, Harvard University; Dr. Horace G. Richards and Dr. Earl A. Shapiro, Academy of Natural Sciences of Philadelphia; Dr. Myra Keen, Department of Geology, Stanford University; Dr. J. Wyatt Durham and Mr. J. H. Peck, Jr., Museum of Paleontology, University of California at Berkeley; Mr. Fred C. Ziesenhenné, Allan Hancock Foundation, University of Southern California; Dr. W. D. I. Rolfe, Hunterian Museum, University of Glasgow; Dr. H. W. Ball and Dr. H. G. Owen, British Museum (Natural History); and Dr. Colin Forbes, Sedgwick Museum, Cambridge University.

Fossil specimens were loaned by Dr. Pedro J. Bermúdez, Dirección de Geología, Ministerio de Minas e Hidrocarburos, Caracas, Venezuela; Prof. Norman E. Weisbord, Department of Geology, Florida State University; Dr. Fernando Moitinho de Almeida, Director, Serviços Geológicos de Portugal; and Mr. Barry Roth, California Academy of Sciences, San Francisco.

Mr. David G. Stephenson, Department of Geology, University of Keele, Staffordshire, during a visit to his laboratory, allowed me full access to his Kenya material, type-specimens of the Maltese species *Cidaris melitensis* Wright which he had borrowed from the Bristol Museum in anticipation of my visit, and casts of some Duncan and Sladen specimens.

Dr. Marian H. Pettibone, National Museum of Natural History, Smithsonian Institution, facilitated in invaluable ways my working visits to the Smithsonian, helped me obtain some needed references, clarified several taxonomic procedures, and through the years cheered me on.

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Mrs. Evangelina Hernández, scientific illustrator, Department of Marine Sciences, University of Puerto Rico, Mayagüez, prepared the two text-figures.

My husband, Prof. Charles E. Cutress, counseled during resolution of some of my taxonomic problems and was a constant source of moral and material support.

Dr. J. Wyatt Durham, Dr. David L. Pawson and Prof. Norman E. Weisbord kindly reviewed the manuscript and offered many valuable suggestions. Dr. Peter R. Hoover, Director, Paleontological Research Institution, Ithaca, New York, meticulously and ably edited the manuscript, improving it in many ways.

PREVIOUS WORK

Michelin (*in* Duchaissaing, 1855) listed *Cidaris metularia* as a fossil from Guadeloupe. Guppy (1866) referred an Anguillan cidaroid to *Cidaris melitensis* (Forbes) Wright, a Maltese species. Cotteau (1875), working primarily with specimens collected in Anguilla and St. Bartholomew by P. T. Cleve, described as new species *Cidaris clevei*, *Cidaris anguillae* and *Cidaris loveni*.

Jackson (1922), in his monograph on West Indian echinoids, included descriptions and illustrations of the above-mentioned species, recorded *Cidaris tribuloides* (Lamarck) from the Miocene of Cuba, and added two new cidaroid species, *Cidaris peloria* from Puerto Rico and *Cidaris foveata* from Jamaica, and two indeterminate species, *Cidaris* sp. a and *Cidaris* sp. b from Puerto Rico.

Hawkins (1923) referred a test fragment from the Cretaceous of Cuba to *Leiocidaris* sp., and Hawkins (1924) referred another, from the Eocene of Jamaica, to *Cidaris* sp.. Lambert *in* Lambert and Thiery (1909-1925) described *Rhabdocidaris sanchezi* and *Cidaris cubensis*, apparently from specimens from Cuba supplied by M. Sánchez Roig. In Sánchez Roig's 1926 paper on Cuban echinoids, Lambert described *Leiocidaris cojimarensis* and *Leiocidaris leoni* from Sánchez Roig's specimens. Sánchez Roig, in the same paper, mentioned an unnamed *Cidaris* species.

Arnold and Clark (1927) referred specimens to *C. loveni* Cotteau and *C. melitensis* (Forbes) Wright and described as new *Cidaris gymnozona*. Lambert (1931a) described *Dorocidaris molineti*.

Sánchez Roig (1949) cited previous Cuban records and described *Dorocidaris demujiensis*, *Dorocidaris madrugensis*, *Leiocidaris madrugensis*, *Leiocidaris spinidentatus*, *Goniocidaris habanensis* and *Goniocidaris holguinensis*. Sánchez Roig (1952, 1953) added *Dorocidaris garciai* and *Prionocidaris lopezi*.

Gordon (1963), in a paper on Middle Tertiary echinoids of Puerto Rico, recorded unnamed single species of both *Cidaris* and *Phyllacanthus*. *Eucidaris tribuloides* (Lamarck) was recorded from the Pleistocene of Venezuela by Maloney and Macsotay (1968) and by Weisbord (1969), who dated some of his specimens as Pliocene.

Although Brazil is not here considered part of the Caribbean, *Cidaris branneri*, described from that country by White (1887), is included because specimens from Venezuela recorded as *Cidaris* sp. by Osten* (1957) and an unpublished specimen collected by B. Brown in Guatemala may belong to that species.

Some of the above species are mentioned in other papers: Etheridge (1869), Guppy (1867, 1882), Döderlein (1887), Gregory (1891, 1892), Dickerson and Kew (1917), Lambert (1922), Vaughan (1922), Israelsky (1924), Mortensen (1928a, b), Sánchez Roig (1930), Maury (1936), Jackson (1937), Brodermann (1949), Casanova (1955), Cooke (1961), and Brito and Ramires (1974b). Most of the species are assigned here to other genera and some are assigned to other species. The original names are indexed so that the pertinent species discussions can be located in the text.

COLLECTING LOCALITIES

In the "Material" lists in the "Systematics" section, localities are cited only by number, *e.g.*, Bermúdez 54, Palmer 1452, USGS 5355. The complete locality data are given below with localities grouped under the name of the collector(s). Letter designations for unnumbered localities are introduced here for convenience in citing these localities in the "Systematics" section.

Data for the Palmer localities were taken from Palmer (1948). USGS locality data were copied from the register catalogues maintained by the U.S. Geological Survey, Washington, D.C. Informa-

*Deletion in the text of this paper of particles for the names **da Veiga Ferreira, de Loriol, van den Bold** and **von der Osten** was an editorial decision, not the author's preference.

tion for all other localities was taken from labels with specimens. It should be noted that Santa Clara Province, Cuba (used by Palmer) is the same as Las Villas Province (used by Bermúdez).

In recent years, dates for Caribbean strata younger than Eocene have generally been moved upward in time. There is not yet complete agreement on some of this redating. Because of this, some species assignments for similar specimens from geographically separated areas proved difficult. Where possible, the formation at a locality is given. Formation names without brackets in the locality data are according to the collector; those in brackets are my additions, based on more recent, secondary sources. The abbreviation "CC.," used by both Bermúdez and Palmer, refers to the Carretera Central.

LOCALITIES GROUPED BY COLLECTORS

B. W. Arnold

- (a) — Unnumbered; Jamaica; yellow limestone, probably the Cambridge Formation of R. T. Hill, with no detailed locality; Eocene.
- (b) — Unnumbered; Jamaica; no other data given.
- (c) — Unnumbered; Jamaica; base of road cut west side of road, 700-800 feet beyond Spring Mount, St. James Parish.
- (d) — Unnumbered; Jamaica; on earth on a banana plantation in the region of Seven Rivers, near the Great River, not far from Cambridge, St. James Parish.
- (e) — Unnumbered; Jamaica; in vicinity of Easington, just west of the Yallah River, on high elevation.
- (f) — Unnumbered; Jamaica, 1886.

P. J. Bermúdez

- (a) — Unnumbered; Cuba, Las Villas Province; 7.5 km N.E. Sancti Spiritus; upper Eocene.
- (b) — Unnumbered; Cuba, Pinar del Río Province; Río Hondo, near Wilfredo Fernandez house; lower Oligocene [near **Palmer D103**].
- (c) — Unnumbered; Cuba, Las Villas Province; El Capiro quarry, Santa Clara; Upper Cretaceous, Habana Formation.
- (d) — Unnumbered; Cuba, Las Villas Province; 1 km E. of railroad station on road to Tarafa; Upper Cretaceous, Habana Formation.
- (e) — Unnumbered; Cuba, Las Villas Province; La Marota; Upper Cretaceous, Habana Formation.
- 5 — Cuba, Matanzas Province; cut on CC. just W. of Nena Machado Hospital, Matanzas; middle Miocene; = **Palmer 898P** [Canímar Formation].
- 26 — Cuba, Matanzas Province; km post 118.5 east of Matanzas City on highway; Upper Cretaceous [San Luis Formation].
- 39C — Cuba, Matanzas Province; Los Molinos, km post 94 highway Habana to Matanzas; middle Miocene [Canímar Formation].
- 48 — Cuba, Matanzas Province; Tejar el Abra, Abra de Yumurí; upper Oligocene, Cojimar Formation.
- 54 — Cuba, Matanzas Province; km post 100 on road Habana to Matanzas; middle Miocene [Canímar Formation].

- 76A — Cuba, Habana Province; Madruga, Central San Antonio; Paleocene, Madruga Formation [type locality of formation].
- 83 — Cuba, Matanzas Province; Tejar Zayas, Matanzas; upper Oligocene, Cojímar Formation.
- 110 — Cuba, Matanzas Province; 250 m N.W. of Penon, 7 km S. of Marti; middle Eocene [Loma Candela Formation].
- 147 — Cuba, Las Villas Province; 1 km S. of Turbina, Central Constancia; middle Miocene.
- 148 — Cuba, Las Villas Province; 1 km W. of Baños, Ciego Montero; Upper Cretaceous, Habana Formation.
- 154 — Cuba, Las Villas Province; cliff N. 55° W. of Pinar, 8 km N. 76° E. of Tamarindo; upper Eocene.
- 163 — Cuba, Las Villas Province; 0.5 km W. of Jicotea; upper Eocene [Jabaco Formation].
- 185 — Cuba, Las Villas Province; 2 km S. of Palmira on road to Cienfuegos.
- 229 — Cuba, Habana Province; 1 km S. of Estación F. C. C. Hershey, La Loma Cojímar; upper Oligocene, Cojímar Formation.
- 230 — Cuba, Habana Province; Finca Velazco, road Cojímar to Guanabacoa; upper Oligocene, Cojímar Formation.
- 234 — Cuba, Habana Province; Cantera Atturas de Almendares; upper Oligocene, Cojímar Formation.
- 246 — Cuba, Pinar del Río Province; Loma Candela, San Diego de los Baños; middle Eocene, Loma Candela Formation.
- 261 — Cuba, Pinar del Río Province; Loma Candella, San Diego de los Baños; middle Eocene, Loma Candela Formation [type locality of formation].
- 299 — Cuba, Matanzas Province; Abra de Yumurí; upper Miocene.
- 302 — Cuba, Pinar del Río Province; Noroña; lower Oligocene.
- 324 — Cuba, Matanzas Province; 0.5 km S. of Central Saratoga; middle Eocene.
- 337 — Cuba, Pinar del Río Province; 4.5 km W. of Guanajay on road to Mariel; upper Eocene, Jabaco Formation [type locality of formation].
- 400 — Cuba, Habana Province; 1.4 km N. of Punta Brava; Upper Cretaceous.
- 526D — Cuba, Pinar del Río Province; 4 km W. of Guanajay; upper Eocene.
- 604 — Cuba, Pinar del Río Province; Loma Candela; middle Eocene, Loma Candela Formation.
- H-15,262 } { Dominican Republic; Mioncion-Mao road; middle Miocene,
H-15,265 } { Gurabo Formation.
- H-15,448 — { Dominican Republic; Río Cana; middle Miocene, Gurabo
Formation.
- H-15,462 } { Dominican Republic; Sabaneta-Los Quemados road; middle
H-15,468 } { Miocene, Gurabo Formation.
- H-15,473 } { Dominican Republic; km 8 on road El Palenque, San Cristobal;
H-20,093 — { upper Oligocene.
- B. Brown**
(a) — Guatemala; Santa Amelia. 1948.
- P. T. Cleve**
(a) — Unnumbered; Anguilla; Anguilla Formation.
(b) — Unnumbered; St. Bartholomew; St. Bartholomew limestone.
- C. W. Cooke**
C-25-19 — Dominican Republic [see **USGS** 8519].
C-93-55 — Puerto Rico [see **USGS** 19700].

C. W. Cooke

- C-112-55 — Puerto Rico [see **USGS** 19714].
 C-116-55 — Puerto Rico [see **USGS** 19718].
 C-119-55 — Puerto Rico [see **USGS** 19720].
 C-166-55 — Puerto Rico [see **USGS** 19760].
 C-206-55 — Puerto Rico [see **USGS** 19795].
 C-255-55 — Puerto Rico [see **USGS** 19837].

B. M. Cutress

- 1 — Puerto Rico; highway 129, Arecibo to Lares; cut in private road just off highway near km post 31; Lares Formation.
 2 — Puerto Rico; highway 2, km 243.6, just west of Río Tallaboa; cut on north side of highway; yellow fossiliferous limestones; Ponce Formation.

K. W. Earle

- (a) — Unnumbered; Anguilla; upper Eocene; probably Anguilla Formation.

W. A. Gordon

- (a) — Unnumbered; Puerto Rico, Cibao marl, Quebradillas quadrangle; at points along the side track from route PRI 446 at km 6.5.

P. Martin-Kaye

- GR-222699 — Antigua; disused quarry in ex-U. S. Army base, inside of small hill near disused hospital 47 ft. above sea level; MK 111; Antigua Formation.

New York Academy of Sciences — American Museum of Natural History (NYAS-AMNH)

- 20 — Puerto Rico; government road, San Sebastian to Lares, shaly limestone, south side of road, km post 33 (11 km E. of San Sebastian or 5 km W. of Lares); "Arecibo" Formation [Lares Formation].
 56 — Puerto Rico; government road, San Sebastian to Lares, km post 33, marly beds, base of "Arecibo" Formation [Lares Formation].
 58 — Puerto Rico; government road, San Sebastian to Lares, km post 33, collected from north side of road from excavations where road metal had been quarried; base of "Arecibo" limestone [Lares Formation].
 105 — Puerto Rico; Collazo shales, government road, San Sebastian to Lares, near km post 20 [Lares Formation].
 117 — Puerto Rico; weathered marl, government road, Aguadilla to Rincon, km post 2, from roadside grottoes where road metal had been taken out; geologic age not known, Arecibo limestone; C. A. Reeds, collector. [Present km 2 on this road is near Añasco where there are neither quarries nor marls; locality may be between present km 21 and 23 where there are several quarries; these are in Cibao limestone.]
 195 — Puerto Rico; 2 km S. W. of Juana Díaz, from fallen block of limestone alongside of the irrigation flume on flood-plain of the Jacaguas River; geologic age not known, probably Miocene, Ponce chalk; C. A. Reeds, collector [Juana Díaz Formation].

Oberlin College (formerly part of their collections; collector unknown)

- (a) — Jamaica; Ceran Hill, Port Maria; Eocene.

R. H. Palmer

- (a) — Unnumbered; Cuba, Camagüey Province; cut just W. of Grúa 10, Ramal Juan Crillo Central, Jatibonico Cave Railroad, 1938 [= **Palmer** 1452].
 51a — [See **UCMP** B-3254].
 PC52 — Cuba, Santa Clara Province; Finca de Don Arcadis; Foraminifera section; *Barretia* fragment; Eocene.

- 53 — Cuba, Santa Clara Province; ls, hard, brittle and light gray; Loma Macagua, 1 km W. of Esperanza; 6/10/29 [= **Bermúdez** 81; Jabaco Formation].
- 72 — Cuba, Santa Clara Province; foraminiferal sand, La Vega-Carretera Central crossing, 5 km N.W. of Esperanza; 6/20/29.
- 75 — Cuba, Santa Clara Province; earth with many large Foraminifera, Finca La Casimba, 3.5 km N.W. of Jicotea on Carretera Central; 6/20/29.
- D103 — Cuba, Pinar del Río Province; loc. N. of San Cristobal, ca. 200 m E. of house of Wilfredo Fernandez, Finca Echevarria on S. edge of La Hoya in Río Honda, near San Cristobal [near **Bermúdez** (b)].
- 115 — Cuba, Santa Clara Province; limestone and lime as in Tarafa R.R. cut 1 km N. of Santa Clara; Upper Cretaceous; 7/12/29.
- 165 — Cuba, Santa Clara Province; N.E. of San Juan de las Yeras, 2 km; locality where asphalt is reported; specimens are from a ls. outcrop; there are numerous small cavities lined with a dark substance resembling asphalt; 10/16/29.
- PC188 — [See **UCMP B-3499**].
- 377 — Cuba, Matanzas Province; S.E. end of Yumurí Gorge, in back of Standard Oil station; highest beds; on N. side; 5/9/30.
- 378 — Cuba, Matanzas Province; N.W. end of Yumurí Gorge series, on N. side; lowest; 5/10/30.
- 405 — Cuba, Habana Province; white marl at base of Cojímar Gorge, south end; upper Oligocene; 6/7/30; [= **UCMP B-3286**; Cojímar Formation].
- 405A — Cuba, Habana Province; old kiln at 405.
- 491 — Cuba, Camagüey Province; ls. chips and soil; from hill at Mabuya W. of Chambas; upper Eocene; 12/7/30.
- 591 — Cuba, Camagüey Province; large *Lepidocyclus*; W. de Ciego, 42 km; km 419.7 on CC.; Oligocene; 2/11/31.
- 601 — Cuba, Camagüey Province; W. of Ciego, 45 km; note large *Lucina*; 2/18/31.
- 687 — Cuba, Camagüey Province; casts, 15 mi. E. of Camagüey on Maraguan road from Guanabanito River to 2 km E.; Eocene; 5/28/31.
- 727 — Cuba, Camagüey Province; Cuartel hill S. slope, just W. of Nuevitas; 8/27/31.
- 757 — Cuba, Habana Province; cut under R.R. bridge 2 km W. of Madruga at Central San Antonio; Upper Cretaceous; notable locality; 10/15/31 [= **UCMP B-3290**, Big Boulder Bed; this is member of Habana Formation].
- 812 — Cuba, Habana Province; Cretaceous directly under chalk, 1+ km S. of Central San Antonio in railroad cut; 1/14/32.
- 813 — Cuba, Habana Province; Loma la Tierra, 19.5 km S.E. of Havana; cavernous ls; brick yard; 1/15/32.
- 832 — Cuba, Habana Province; Foraminifera and large rudistid fragment, 1 km S.W. of Madruga; *Titanosarcolithes*; Upper Cretaceous; 1/27/32.
- 835 — Cuba, Habana Province; big boulder bed, 900 m S. of Madruga; Upper Cretaceous; 1/30/32 [Habana Formation].
- 864 — [See **UCMP B-5231**].
- 888 — Cuba, Habana Province; lime gravel, S. edge of Mantilla, Calle Libertad, Reparto Los Tunos; Upper Cretaceous [Habana Formation].
- 894 — Cuba, Habana Province; Cretaceous chalk within? cone sandstone, 500 m N.W. of Marabú road crossing of Río San Marcos on road to La Luz [Habana Formation].

R. H. Palmer

- 895P — Cuba, Habana Province; N. of Grua Esperanza, 150 m, which is 6 km E. of Madruga.
- 898P — Cuba, Matanzas Province; cut on CC. just W. of Nena Machado Hospital [= **Bermúdez** 5].
- 926 — Cuba, Matanzas Province; CC. cut, approximately 4 km S.W. of Matanzas near km post 100 (97) from Habana; gravel equivalent to upper Yumuri.
- 932 — Cuba, Matanzas Province; CC. approximately 8 km W. of city or Km 94 plus 100 m; Upper Yumuri. 9/11/32.
- 942 — Cuba, Habana Province; Tejar Consuelo (of Mato) La Cienaga, Reparto Cerro, Habana, 1.3 km east of Tropical Brewing Co., N.E. of Puentes Grandes; upper Eocene; 7/15/32 and 8/17/32 [= **Bermúdez** 36, which is type locality of Consuelo Formation].
- 965 — [See **UCMP** B-3404].
- 976 — Cuba, Habana Province; tan and white marl directly over Cretaceous, 1.5-2.5 km W. of Cojimar on the carretera to Casa Blanca; Cojimar Formation.
- 978 — Cuba, Habana Province; marls in deep road cut across hill $\pm$ 1 mi. N.E. of Casa Blanca; Basal Yumuri beds; 8/27/32.
- 997 — Cuba, Habana Province; soft cavernous ls. material, Cantera Toledo, 200 m W. of 996, 1 km E. of Jockey Club, Marianao.
- 1003 — Cuba, Pinar del Río Province; N. of CC. 2.1-2.2 mi., on road to San Diego de los Baños; Eocene ss.
- 1018 — Cuba, Habana Province; marl 2 km S.W. of Cojimar on Hershey Electric R.R.; Basal Yumuri; 10/16-30/32.
- 1024 — Cuba, Habana Province; S. face of hill 750 m E. of Cojimar Gorge above "Villa Real"; lower cavernous ls.; 11/6/32.
- 1025 — Cuba, Habana Province; basal marls in Cojimar Gorge, on E. side on road to Finca Noria; Cojimar Formation; 11/6/32.
- 1026 — Cuba, Habana Province; above Río Almendares in Reparto Kohly, just S. of Riverside Yacht Club.
- 1027 — Cuba, Camagüey Province; Loma Calixto, Nuevitas; gifts from Hno. Leon, Dr. Mario Sánchez Roig and N. D. Chawner [= **Weisbord** 2].
- 1028 — Cuba, Habana Province; cliff E. side of Río Almendares opposite Riverside Yacht Club.
- 1030 — Cuba, Habana Province; lowest Eocene, 200 m approximately, S. of 1026 W. side of Almendares River in Reparto Valley.
- PC1032 — [See **UCMP** B-3408].
- 1034 — Cuba, Camagüey Province; CC. cut, both sides, 425.5 km E. of Habana or 36.1 km W. of Ciego; marly ls; 1/25/33.
- 1040 — Cuba, Oriente Province; CC. cut km 742.7 E. of Habana or 48 km E. of Tunas; yellow marl; lower ? Oligocene.
- 1041 — Cuba, Oriente Province; quarry N. of CC. at km 743.2 or 48.5 km E. of Tunas; marly yellow ls.; lower Oligocene; 1/28/33.
- 1042 — Cuba, Oriente Province; CC. cut km 744.8 E. of Habana at Las Calabazas, 27.2 km W. of Holguin.
- 1044 — Cuba, Oriente Province; ditch at side of CC. at km 745.4 E. of Habana or 24.5 km W. of Holguin; 1/29/33.
- 1045 — Cuba, Oriente Province; CC. cut km 749 E. of Habana or 23 km W. of Holguin; 1/29/33.
- 1046 — Cuba, Oriente Province; CC. cut km 749.7 E. of Habana or 22.3 km W. of Holguin; 1/29/33.
- 1056 — Cuba, Oriente Province; N. of La Cruz crossing, 1.1 km on narrow gauge railroad, S. of Santiago; 2/1/33.

- 1064 — Cuba, Camagüey Province; N. of Sibanicu, 9.1 km, at Finca Aurora, on road to Vorella; -/4/33.
- 1081 — Cuba, Santa Clara Province; road cuts at Arroyola Palma, 8.2 km S.E. of bridge over Río Zara or 12.8 km of Sancti Spiritus; 2/10/33.
- 1082 — Cuba, Santa Clara Province; CC. cut km 390.5 or 3.8 km E. of Sancti Spiritus; 2/11/33.
- 1085 — Cuba, Camagüey Province; E. of Arroyo Blanco, 150 m, in road to Majagua; 2/12/33.
- 1090 — Cuba, Santa Clara Province; Carretera Central 517 km [sic] N.E. of Sancti Spiritus; Oligocene; 2/13/33.
- 1098 — Cuba, Habana Province; N. of CC. Hershey station on Barreras-Tarara, 700 m, *Miogypsina* beds; 2/26/33.
- 1102 — Cuba, Pinar del Río Province; marls with numerous *Lepidocyclinas* and one *Pauropygus*, 4.65 km W. of Guanajay on road to Mariel; Eocene; 9/3/33.
- 1107 — Cuba, Habana Province; Río Guanabo gorge 14 mi. E. of Habana Harbor; 3/5/33.
- 1117 — Cuba, Santa Clara Province; 2 km (1.25 mi.) N. of Ciego Montero in S. bank of Río Anaya E. of Baños; Upper Cretaceous; 3/11/33.
- 1120 — Cuba, Santa Clara Province; W. of Baños, 1 km in bank of Río Anaya; *Gallowayina*; Cretaceous; 3/11/33 and 3/14/33.
- 1189 — Cuba, Matanzas Province; corner of Calles Santa Rita and Montserrat, Pueblo Nuevo, Matanzas; sand and *Pecten* (*Jamira*).
- 1228 — Cuba, Habana Province; ?Principe chalk? E. of Santiago de Las Vegas, 4 km; 75 m S. of 1095 which is old mine working, stake 1 on Cleopatra claim; 1/29/34 [Principe = Universidad Formation].
- 1245 — Cuba, Habana Province; S. of Gen. Wood asphalt mine, 0.5 km, 1.5 km S.E. of Santa Maria del Rosario, Finca Tamarindo, BBB.
- 1262 — Cuba, Habana Province; Cantera Caimiti, 500 m S. of Cantera Criollo Puentes Grandes; spines; 4/8/34.
- 1320 — Cuba, Habana Province; E. end of R.R. cut, La Ceiba Station, Güines.
- 1393 — Cuba, Santa Clara Province; schists at Finca Cicatero, 6 mi. N. of Trinidad; 12/10/34.
- 1452 — Cuba, Camagüey Province; first cut S. of Clonia Cristales de Jatabonico, cut W. of Grua 10, Ramal Juan Criollo; Oligocene; 2/6/35 [= Palmer (a)].
- 1553 — Cuba, Matanzas Province; km 202 United R.R., or 0.5 km S. of km 213 on CC., 23 km E. of Colón church; *Schizaster*; Oligocene; 7/13/35; [= UCMP B-3493; ?upper Oligocene].
- 1554 — Cuba, Matanzas Province; N. of Colón, 1 km, on road to Banaguises; 7/13/35.
- 1593 — Cuba, Matanzas Province; S. side of Yumurí Gorge, at tannery; 8/3/35.
- 1625 — Cuba, Habana Province; near Sage well; [?] km N.W. of Campo Florida; Upper Cretaceous.
- 1626 — Cuba, Camagüey Province; C. Jatibonico R.R., 500 m S. of CC. crossing on Ramal Juan Criollo; Oligocene-Miocene; 12/16/35.
- 1627 — Cuba, Camagüey Province; N. of CC. crossing, 200 m, on Ramal Juan Criollo; Oligocene; C. Jatibonico; 12/26/35.
- 1635 — Cuba, Camagüey Province; about 150 m (1st cut) N. of switch to Ramal Valle, C. Jatibonico; Oligocene; 12/26/35.
- 1640 — Cuba, Camagüey Province; deep cut N. of Grua 9, Ramal Juan Criollo; Eocene; 12/27/35 [= Bermúdez 481; Jabaco Formation].

R. H. Palmer

- 1719 — Cuba, Southern Santa Clara Province; from Cienfuegos end of Carretera, 2 km (1.2 mi.); high in Oligocene; 5/30/36.
 2191 — Cuba, Pinar del Río Province; N. of CC., 3.35 km, just N. of N. end of Loma Candela which is 3.3 km N. of CC.; 3/19/39.
 2524 — [See **UCMP B-3469**].

N. D. Sohl et al.

- J-66-15 — Jamaica [see **USGS 29544**].
 J-66-55 — Jamaica [see **USGS 29956**].
 J-71-47 — Jamaica [see **USGS 30066**].
 J-71-105 — Jamaica [see **USGS 30424**].

C. T. Trenchmann

- (a) — Jamaica; yellow limestone, Spring Mount; middle Eocene.

U. S. Geological Survey (USGS)

- 20 — Antigua; Hodges Bay, W. R. Forest, collector.
 44 — Antigua; Green Island. W. R. Forest, collector. [Note: the number 6356 on the label with the specimen is not a USGS locality number nor a USNM catalogue number; it is a temporary, unofficial identification number.]
 2213 — Florida, Calhoun County. One mile below Bailey's Ferry on the Chipola River.
 2564 — Florida, Calhoun County. "Burns' typical locality" in the right bank of Chipola River, on the McClelland Farm one mile below the bridge at the old Bailey Ferry, 10 miles west of Blountstown.
 3419 — Florida, Calhoun County. McClelland's Farm on west bank of Chipola River one mile below Bailey's Ferry and new bridge.
 5255 — Cuba; Santiago; fossils received 29 January 1910; Quaternary?
 8519 — Dominican Republic; Santiago Province; left bank Río Mao about 0.5 mi. above the ford at Cercado de Mao; specimens mostly from lower part of the bluff; T. W. Vaughan and C. W. Cooke, collectors; 3 May 1919 [= **Cooke C-25-19**].
 8583 — Trinidad; Mayo Village Quarry; locality 11; F. W. Penney, collector.
 8727 — Dominican Republic, Santiago Province; trail from Potrero toward Las Matas, 7.5 miles out; DC-53; D. D. Condit, collector; 2 May 1919.
 17212 — Puerto Rico; north coastal plain, weathered hard to chalky buff limestone capping hill (402 m elev.) west of Quebrada Los Muertos, NE 1/4, SE 1/4, San Sebastian quadrangle, 0.5 km N. of highways 8 and 13 at a point above 0.6 km N.W. of surfaced road fork, 1.5 km W. of Lares; waxy tan clay at base of hill. This is apparently part of San Sebastian Formation; PR-36. H. R. Bergquist, collector; Dec. 1944 [base of Lares Formation].
 19700 — Puerto Rico; Cumuy quadrangle, km 10.75-10.8 route 129, at hairpin bend 2.2 km from S. edge of quadrangle; Miocene, Cibao limestone? C. W. Cooke and A. D. Watt, collectors; 5/18/55 [= **Cooke C-93-55**; Aguada = Los Puertos limestone].
 19714 — Puerto Rico; Vega Alta quadrangle, S. edge of quadrangle about 4.5 km S.S.W. of Vega Alta, km 1.5-1.6 [? route 677]; Miocene, Cibao or Quebradillas limestone. C. W. Cooke and A. D. Watt, collectors [= **Cooke C-112-55**; Cibao limestone].
 19718 — Puerto Rico; Vega Alta quadrangle, km 5 [? route 647], about 4.5 km S. of Vega Alta; Miocene; Cibao limestone. C. W. Cooke and A. D. Watt, collectors, 5/22/55 [= **Cooke C-116-55**].
 19720 — Puerto Rico; Aguadilla quadrangle, km 148.4 route 2 about 3 km N.E. of Aguada, second hill S. of Río Culebrinas; Miocene, Cibao limestone. C. W. Cooke and A. D. Watt, collectors; 5/24/55 [= **Cooke C-119-55**].

- 19760 — Puerto Rico; Moca quadrangle, km 3.1 to km 3.2 route 112, W. of fork 2.5 km N. of route 111; Miocene, base of Quebradillas limestone. C. W. Cooke and A. D. Watt, collectors; 6/2/55 [= **Cooke C-166-55**; probably Cibao limestone].
- 19795 — Puerto Rico; San Sebastian quadrangle, km 31.6 route 111, 4 km W.N.W. of Lares. C. W. Cooke and A. D. Watt, collectors; 6/9/55; Miocene, Collazo marl; [= **Cooke C-206-55**].
- 19837 — Puerto Rico; Barceloneta quadrangle, route 634 at junction with 642; Miocene, Cibao limestone. C. W. Cooke and A. D. Watt, collectors; 6/19/55 [= **Cooke C-255-55**].
- 29544 — Jamaica; shale exposure on flat below houses and road cuts along Jerusalem Mountain-Belleisle Mountain road about 3,600 feet airline N.E. of road intersection at Jerusalem Mountain Inlier; U. Cretaceous, Maestrichtian. Hayet, Kauffman, Sohl, collectors; 11/66 [= **Sohl et al. J-66-15**].
- 29956 — Jamaica, St. Ann's Parish; St. Ann's Great River Inlier, *Inoceramus*-bearing shales above the first ford and on right bank of St. Ann's Great River; Upper Cretaceous. Sohl, Kauffman, Coates, Hazel, collectors; 12/66 [= **Sohl et al. J-66-55**].
- 30066 — Jamaica; exposures of silty shale similar to those of 30065 but about 120 ft. higher in section, St. Ann's Great River, St. Ann's Inlier; Upper Cretaceous. N. F. Sohl and William Ross, collectors; 1/71 [= **Sohl et al. J-71-47**].
- 30424 — Jamaica; Maestrichtian shale immediately below oyster limestone in road cuts 0.27 mile airline S.S.E. of road junction at Jerusalem Mountain 18° 19' 15" x 78° 13' 52", Jerusalem Mountain Inlier; Upper Cretaceous. E. G. Kauffman and N. F. Sohl, collectors; 12/61 [= **Sohl et al. J-71-105**].

University of California at Berkeley, Museum of Paleontology (UCMP)

- B-3254 — Cuba, Las Villas Province; Finca de Guanajita, 9 km W. of Santa Clara and about 3 km S. of carretera; Upper Cretaceous. R. H. Palmer, collector, **Palmer 51**.
- B-3286 — Cuba, Habana Province; quarry on W. side of Guanabaco-Cojimar road, on S. edge of Cojimar Village; type locality of Cojimar Formation; upper Oligocene. R. H. Palmer, collector, 6/7/30, **Palmer 405**.
- B-3290 — Cuba, Habana Province; cut under R.R. bridge 2 km W. of Madruga at Central San Antonio; notable locality; Upper Cretaceous, Big Boulder Bed. R. H. Palmer, collector, 10/15/31, **Palmer 757** [Habana Formation].
- B-3404 — Cuba, Habana Province; dirty shales and probably the Big Boulder Bed, 200 m W. of Canado Station, Los Angeles (Luyano) back of Lykes Packing Plant in railroad cut; rudistids; Upper Cretaceous. R. H. Palmer, collector, 8/2/32, **Palmer 965** [Habana Formation].
- B-3408 — Cuba, Camagüey Province; 454.7 km E. of Habana, 7 km W. of Ciego; rudistids in platanar [plantain plantation]; Upper Cretaceous, Habana Formation (?). R. H. Palmer, collector, 1/33, **Palmer 1032**.
- B-3469 — Cuba, Las Villas Province; W.N.W. of Central Perseverance, 1.8 km, on road to Aguada, in creek bank of Arroyo Vaquito, to 300 m N. of culvert; Aguada de Pasajeros; Upper Cretaceous. R. H. Palmer, collector, **Palmer 2524**.
- B-3493 — Cuba, Matanzas Province; km 202 on United Railroad of Habana, or 0.5 km S. of km 213 of Central Highway and 23 km E. of Colón church; upper Oligocene (?). R. H. Palmer, collector, 7/13/35, **Palmer 1553**.

(UCMP)

B-3499 — Cuba, Las Villas Province; Jertia Pass through hill from El Ebra to Potrerillo, Central Hormiguero; Cretaceous. R. H. Palmer, collector, **Palmer** 188.

B-5231 — Cuba, Habana Province; *Titanosarcolites*, coral and forams 4.5 km N. of Santa Maria del Rosario on Guanabaco Road; Cretaceous. R. H. Palmer, collector, 3/4/32, **Palmer** 864.

N. E. Weisbord

2 — Cuba, Camagüey Province; Loma Calisto; Eocene [= **Palmer** 1027].

D608 } Venezuela; eastern edge of Playa Grande village at W-30;
D608a } elevation approximately 61 m; granule to pebble gravel; Pleistocene, Abisinia Formation; absolute age, determined by the ionium disequilibrium method, is in excess of 300,000 years.

K599a — Venezuela; bluff 125 m W. of the intersection of the Playa Grande Yachting Club road and coast road, and about 95 m due S. of shoreline; tan, fine-grained, calcareous sandstone; Pliocene, Playa Grande Formation, Catia Member.

C609a — Venezuela; on and near the "Lithothamnium" reef at W-23, north flank of Punta Gorda anticline; reef of calcareous algae with layer of cobbles at base; Pliocene, Playa Grande Formation, Maiquetia Member.

LOCALITIES GROUPED GEOGRAPHICALLY

Anguilla. — **Cleve** (a); **Earle** (a).

Antigua. — **Martin-Kaye** GR-222699; **USGS** 20, 44.

Cuba. — **Bermúdez** (a)-(e), 5, 26, 39C, 48, 54, 76A, 83, 110, 147, 148, 154, 163, 185, 229, 230, 234, 246, 261, 299, 302, 324, 337, 400, 526D, 604; **Palmer** (a), PC52, 53, 72, 75, D103, 115, 165, 377, 378, 405, 405A, 491, 591, 601, 687, 727, 757, 812, 813, 832, 835, 888, 894, 895P, 898P, 926, 932, 942, 976, 978, 997, 1003, 1018, 1024-1028, 1030, 1034, 1040-1042, 1044-1046, 1056, 1064, 1081, 1082, 1085, 1090, 1098, 1102, 1107, 1117, 1120, 1189, 1228, 1245, 1262, 1320, 1393, 1452, 1553, 1554, 1593, 1625-1627, 1635, 1640, 1719, 2191; **USGS** 5255; **UCMP** B-3254, B-3286, B-3290, B-3404, B-3408, B-3469, B-3493, B-3499, B-5231; **Weisbord** 2.

Dominican Republic. — **Bermúdez** H-15,262, H-15,265, H-15,448, H-15,462, H-15,468, H-15,473, H-20,093; **USGS** 8519, 8727.

Florida. — **USGS** 2213, 2564, 3419.

Guatemala. — **Brown** (a).

Jamaica. — **Arnold** (a)-(f); **Oberlin** (a); **Trenchmann** (a); **USGS** 29544, 29956, 30066, 30424.

Puerto Rico. — **Cutress** 1, 2; **Gordon** (a); **NYAS-AMNH** 20, 56, 58, 105, 117, 195; **USGS** 17212, 19700, 19714, 19718, 19720, 19760, 19795, 19837.

St. Bartholomew. — **Cleve** (b).

Trinidad. — **USGS** 8583.

Venezuela. — **Weisbord** D608, D608a, K599a, S609a.

TERTIARY STRATIGRAPHY OF PUERTO RICO AND CUBA

Because there is no consensus concerning names and ages for Tertiary lithological units in Puerto Rico, several viewpoints are briefly summarized here.

The Cuban localities of Dr. Bermúdez and Dr. Palmer include formations that are well documented in Bermúdez' papers (1950, 1963). Because these references are uncommon in libraries, brief information from them is given here. Younger ages should be designated for many of the Cuban Miocene formations, in accordance with zonation work of Bolli and Bermúdez (1965) and Banner and Blow (1965). These revisions, however, have not been made formally except through a few suggested correlations in various reports on Puerto Rican and other Caribbean formations. These correlations are included here as an indication of possible new ages for the Cuban formations.

SOUTHWESTERN PUERTO RICO

Ponce Formation. — Berkey (1915) mentioned "Ponce chalky limestones and marls" of southwestern Puerto Rico. Hubbard (1920, 1923) referred to "Upper and Lower Ponce." Zapp *et al.* (1948) also referred to upper and lower units of the Ponce. Mitchell (1922), in mapping of Tertiary units in southwestern Puerto Rico, included the Juana Díaz outcrops of mudstones in the Ponce Formation. Meyerhoff (1933) separated these sequences into a lower Juana Díaz Formation and upper Ponce Formation. In accordance with their understanding of the original intent of the name, Moussa and Seiglie (1970, 1975) restricted the name Ponce to the yellowish, fossiliferous, chalky limestones of shallow-water, marine origin such as are typically found in quarries 1 and 2 of the Puerto Rico Cement Company at Ponce and various other sites in the Ponce and Río Tallaboa areas of southwestern Puerto Rico. Monroe (1973) also appears to use the name Ponce in this restricted sense.

Planktonic foraminifers, which are useful as index fossils, are lacking in this yellowish limestone, but in quarry 2 the unit overlies a friable sandstone that can be assigned to the *Globigerinatella insueta* - *Globigerinoides sicamus* zone of Banner and Blow (1965). Because of this position and the presence of *Gypsina pilaris* and *Globigerinoides ruber* in the yellow limestone, Seiglie and Bermúdez (1969) dated the formation as middle to late Miocene, and Bermúdez and Seiglie (1970) believed it to be equivalent to the middle and (or) upper member of the Camuy (= Quebradillas) Formation of northern Puerto Rico and to be correlated with the Gurabo Formation of northern Dominican Republic. Seiglie and Moussa

(1975) dated the middle and upper members of the Quebradillas as Pliocene. Moussa and Seiglie (1975) found *Miogypsina*, which lived from the late Oligocene through the Miocene, in the lower part of the formation and suggested the age of that part extends back in time beyond the early - middle Miocene boundary.

Through study of the ostracod fauna, Bold (1966, 1969) indicated a late Miocene age for the Ponce. He found similarities between its fauna and those of the Yaque Group of the Dominican Republic, the Springvale Formation of Trinidad, and the upper Tubará Formation of Colombia and suggested the formation was deposited in warm, shallow (not over 50 feet), purely marine waters. Macsotay (1972), on the basis of molluscan taxa, listed the Ponce as Pliocene, correlatives including the Bowden shell bed, and the Mao, Tamiami and Pinecrest Formations.

Juana Díaz Formation.—The Juana Díaz shales of Berkey (1915) were named as a formation by Mitchell (1922) in his columnar section (pl. 7) but were included in the Ponce Formation in his text p. 260. As mentioned above, Meyerhoff (1933) separated out the Juana Díaz Formation. As considered by Moussa and Seiglie (1970, 1975) and Seiglie and Bermúdez (1969), the formation comprises mudstones, claystones and interbedded marls like those exposed in the bluffs of the Río Jacaguas northwest and southwest of Juana Díaz. These apparently contain a planktonic fauna and were deposited in water 300 m or more deep. Thin beds of limestone within the formation, according to Moussa (1977), comprise bioclastic grains, remains of organisms indigenous to shallow-water environments, and were apparently displaced into deep water by sediment gravity flow.

Moussa and Seiglie's use of the names Ponce and Juana Díaz leaves several lithological units between the two formations, at least two of which they (1970, 1975) believed may warrant formation rank, although they declined to name either unit formally until further data are obtained. Seiglie and Bermúdez (1969) referred informally to the lower unit as "Angola limestone." Monroe (1973) included in the Juana Díaz those units that lie between Moussa and Seiglie's Juana Díaz and the base of the Ponce Formation.

Seiglie and Bermúdez (1969) placed the Juana Díaz, as limited by Moussa and Seiglie, in the *Globigerina ampliapertura* and *Tur-*

borotalia opima opima-Globigerina ciperoensis ciperoensis zones and considered it to be of Oligocene age. Bold (1969), on the basis of ostracods, also indicated an Oligocene age and a deep water depositional environment for the Juana Díaz.

NORTHERN PUERTO RICO

Hubbard (1923) listed five units (mentioned in earlier papers by Berkey), arranged here from the youngest to oldest (the first (top) four were combined as the "Arecibo Group"):

Quebradillas limestone. — Hard, pink, semi-crystalline, cavernous to soft, chalky limestones, low in argillaceous material; fossils characteristically in isolated "pockets."

Los Puertos limestone. — Massive, hard, white or pink, semi-crystalline, very cavernous limestone, in many places thin-bedded, with alternate hard and soft layers; fossils scarce.

Cibao limestone. — Soft, white or yellow, chalky, or argillaceous limestone; fossils abundant but poorly preserved.

Lares Formation. — Massive reef type limestone, locally thin-bedded and chalky; limestone grades into shales, clays and gravels in west.

San Sebastian shale. — Green marl, lime sand (marine), fluvatile gravels, lignite blue clays, shaly limestone, and carbonaceous shale.

Aymamon limestone and *Aguada limestone*. — Zapp *et al.* (1948) referred to both Quebradillas and Los Puertos limestones as Aymamón limestone and used the term Aguada limestone for beds assumed to lie between the Aymamón and Cibao limestones, although the type locality of the Aguada apparently lies within an outcrop of the Cibao. They also combined Hubbard's Cibao, Lares and San Sebastian in a "Río Guatemala group." Monroe (1968) noted that the "Aguada" was essentially the base of Hubbard's Los Puertos limestone but chose to retain the name and designated a reference section. Moussa and Seiglie (1975) viewed the "Aguada" concept as unacceptable and indicated that the "Aymamón" comprises beds that are transitional between the Quebradillas and Los Puertos limestones.

Camuy Formation. — Monroe (1963, 1967) mapped as Camuy Formation areas comprising Quebradillas limestone and chalky and marly beds at the top of the Los Puertos limestone. Moussa and

Seiglie (1975) suggested that because the "Camuy" is essentially Hubbard's Quebradillas, because the "Aymamón" includes most of the Los Puertos, and because the upper limits of the Los Puertos were never established by Hubbard, the names Quebradillas and Los Puertos, having priority, should be retained and that redefining the limits between them would not violate rules of the stratigraphic code.

Mucarabones sand.—According to Monroe (1973), another formation exposed near San Juan, the Mucarabones sand, is the clastic equivalent of the Lares Formation and most of the Cibao limestone.

Bermúdez and Seiglie (1970), in studies of planktonic foraminifers in areas mapped by Monroe as Camuy Formation, found that the lower member is equivalent to the *Sphaeroidinellopsis subdehiscens* - *Globorotalia tumida tumida* zone of Banner and Blow and the approximate equivalent of the *Globorotalia dutertrei* - *Globigerinoides obliqua extrema* zone of Bolli and Bermúdez and correlative with the uppermost Pozón Formation of Venezuela. Berggren (1973, fig. 1) assigned the Banner and Blow zone to the earliest Pliocene. The few recrystallized specimens found by Bermúdez and Seiglie in the upper member indicate that part of the formation may be as young as Pliocene. They cited the relative abundance of *Gypsina globulus* in the fore-reef facies of the formation as indicative of late Miocene or Pliocene age. They correlated the middle and upper members of the Camuy with the Ponce Formation of southwestern Puerto Rico, the Gurabo of northern Dominican Republic, the upper part of "Gypsina beds" of western Cuba, the lower Bowden series, upper Bluff Bay series of Jamaica, and, in Venezuela, with the Ojo del Agua Formation and with the upper part of the Cerro Verde Member and part of the Cerro Negro Member of the Cabagua Formation.

In 1975, Seiglie and Moussa reported that studies of borings at Islote, in the north central part of Puerto Rico, showed that the lowest part of the Camuy (= Quebradillas) is latest Miocene. They presented evidence that the lower Quebradillas was deposited in deep water; oyster shells found within these globigerine limestones were thought to be of allochthonous nature. They considered the middle part of the formation to represent an apparent fore-reef environment

or reef talus and the upper part to have been deposited on a narrow shelf where back-reef environments were limited or absent.

Bold (1969) did not indicate an age for the Camuy, but, using ostracods, indicated ages for other units; lower late Miocene for the Aymamón, middle Miocene for the Aguada and upper part of the Cibao, early Miocene for the Lares and Oligocene for the San Sebastian.

On the basis of molluscan taxa, Macsotay (1972) dated the Los Puertos as middle Miocene and his correlations included, among others, the Tamana and Chipola Formations and parts of the Gatún and Manzanilla. He listed parts of the Camuy as late Miocene, his correlations including the Gurabo, Gatún and Manzanilla Formations and the Savanela Member of the Springvale Formation. Upper parts of the Camuy he assigned to the Pliocene, with correlatives including upper parts of the Chagres, Gatún, Gurabo and Springvale Formations.

Monroe (1973) considered the San Sebastian, the Lares and the lower part of the Cibao to be Oligocene, believing that the *Mio-gypsina gunteri* and *Lepidocyclina (Eulepidina) undosa* found in the San Sebastian were restricted to the Oligocene; however, the ranges of these two are now known to extend into the early Miocene. Mousa and Seiglie (1975) dated both the San Sebastian and Lares as Oligocene to early Miocene and the base of the Cibao as late early Miocene or middle Miocene; they did not indicate an upper age limit for the Cibao except to note that in the upper part they found *Marginopora matleyi*, which ranges from late early Miocene probably to the Pliocene.

CUBA

The following brief discussion was taken from Bermúdez (1950, 1963) unless otherwise noted. Bermúdez has given more complete data with bibliographic citations. The formations are listed here from youngest to oldest.

Canímar Formation (Bermúdez, 1950). — Strata that are exposed in the canyon of the Canímar River and extend laterally, occupying a large portion of the Almendares - San Juan syncline in Matanzas Province. Lithologically the formation consists of a coastal calcareous conglomerate with a large quantity of marl and cream-colored, calcareous sand. It is richly fossiliferous. The abundant

foraminifera are benthic forms from moderately deep water. Bermúdez (1963) considered the formation to be of middle Miocene age but now considers it younger (pers. comm., 1975). Deposits of large numbers of *Gypsina pilaris* (Brady) [= *Gypsina globulus* (Reuss)] within the formation have been referred to as "Gypsina beds." These specimens of *Gypsina* serve to correlate the formation also with the Ponce Formation and middle and (or) upper members of the Quebradillas Formation in Puerto Rico (Seiglie and Bermúdez, 1969), both of which have been assigned to the Pliocene (Seiglie and Moussa, 1975). Iturralde-Vinent (1969) included the "Gypsina beds" in the upper Miocene strata within his "Lithofacies Complex II."

Güines Formation (Palmer, 1934). — Strata of hard, massive, crystalline, white and rosy limestones, very cavernous and carrying, in places, deposits of molluscs, coral and other fossils of marine origin. The formation extends to all parts of the island. It includes the "Yumurí limestones" in the valley of the Yumurí River of Matanzas Province. In some sites the limestone is resistant to erosion and forms hillocks on both sides of the Habana-Matanzas anticline. The fauna of the formation indicates deposition in moderately deep water over the insular shelf. Bermúdez (1963) placed the formation above the Cojímar and under the Canímar and dated it as middle Miocene. He correlated it (Bermúdez, 1950) with the following formations: the Tuxpan of Mexico, the Chipola of Florida, the Cercado of the Dominican Republic, the Las Cahobas of Haiti, and the base of the Gatún of Panama and Costa Rica.

Iturralde-Vinent (1969) correlated this formation with the lower to middle Miocene sequences in his "Lithofacies Complex I" and included it in his "Lithofacies Complex II and IV." Bold (1966) correlated the Güines with the Aguada (= Los Puertos) of Puerto Rico, which he (1969) dated as middle Miocene.

Cojímar Formation (Palmer, 1934). — Calcareous marls that are exposed in the north flank of the Habana - Matanzas anticline. The upper part of the formation is the most calcareous, in some places being compacted into limestones; the lower part is more marly. The rich fauna indicates deep-water deposition. Bermúdez (1963) dated the formation as early to middle Miocene and correlated it with four formations: the Cipero of Trinidad, the Trin-

chera of the Dominican Republic, the Thomonde of Haiti and part of the Carapila of Venezuela.

Bold (1965) indicated the Cojímar as including the *Globorotalia fohsi fohsi* zone and correlated it with the Cibao Formation of Puerto Rico. Iturralde-Vinent (1969) included the Cojímar in the strata of pelagic origin in a lower Miocene sequence in his "Lithofacies Complex II," which he believed extends from the *Catapsidrax dissimilis* zone to the top of the *Globorotalia fohsi lobata* zone.

Consuelo Formation (Bermúdez, 1950). — The highest of the upper Eocene strata that are well exposed in the vicinity of La Habana and are present on both flanks of the Habana-Matanzas anticline and lithologically comprise soft, cream-colored, calcareous marls. The formation is correlated with the upper part of the Chapapote Formation of Mexico and the Jackson Formation of the United States.

San Luis Formation (Taber, 1934). — Soft marls of cream or yellowish color, calcareous shales, a little marly limestone and some coastal conglomerate with calcareous matrix encountered near San Luis, Oriente Province and around Guantánamo. The formation was deposited early in the late Eocene but in shallower water than the Jabaco Formation (discussed below). Most of the foraminifera occur also in the Temporal (Guayabal) and Chapapote Formations of Mexico, of middle Eocene (Claiborne) and late Eocene (Jackson) age, respectively.

Jabaco Formation (Bermúdez, 1937). — The lowest stratum in the upper Eocene in Pinar del Río Province. The formation is also exposed in all the other provinces. It is lithologically diverse, deposition having occurred in several environments.

Bermúdez (1950) distinguished as the Jicotea Member deep-water deposits typically exposed about a kilometer east of Jicotea in Santa Clara Province and lithologically consisting of yellowish, calcareous marls with abundant calcareous sand. The Jicotea Member is well-stratified and in places is compacted into marly limestones. Bermúdez correlated the member with the Avon Park Formation of Florida.

Loma Candela Formation (Bermúdez, 1950). — Strata that directly overlie the Universidad Formation (mentioned below) but are separated from it by a large [*gran* of Bermúdez] disconformity.

It is found in all the provinces of Cuba and consists of limestones, yellowish calcareous marls and coastal conglomerates with a matrix of yellowish calcareous marl and fine calcareous sand. In the type locality, there is great lithological diversity, but conglomerates of coastal origin predominate. At other sites, the formation occurs as disintegrated or consolidated calcareous gravel containing abundant fossils. Bermúdez considered it of middle Eocene age and correlated it with the Guayabal Formation of Mexico and Tallahassee and Lake City Formations of Florida.

Universidad Formation (Bermúdez, 1937).—Thick strata of yellow-white, light, soft, calcareous marls that are exposed on both flanks of the Habana - Matanzas anticline and are found elsewhere over the rest of the island. The formation rests on the Capdevila Formation. Bermúdez (1950) distinguished as the Toledo Member white marls comprising principally radiolarians. The Universidad Formation is early Eocene in age and correlates with the following formations: the Aragón of Mexico, the Wilcox of the United States, and the Abujot of Haiti and Santo Domingo. It is the same as the Principe Formation of Palmer (1934).

Capdevilla Formation (Palmer, 1934).—Series of clays and sandstones of chocolate color that crop out in various localities in Habana and Pinar del Río provinces. The formation lies between the Paleocene Madruga Formation and lower Eocene Universidad Formation and was dated as early Eocene and correlated with the Wilcox Formation of the United States by Bermúdez (1950).

Madruga Formation (Lewis, 1932).—Strata in Habana and Pinar del Río provinces that consist of chocolate-colored shales with some calcareous deposits. The formation contains abundant small boulders that appear to have been redeposited from Late Cretaceous strata. The Madruga Formation is Paleocene in age and is correlated with the Midway of Texas.

MORPHOLOGICAL CHARACTERS OF CIDAROIDS

TERMINOLOGY

The terms for the characters referred to in the "Systematics" section of this paper are, for the most part, those of Mortensen (1928b, p. 9) and Fell (1966, p. U313) and are fully detailed in those papers. Rather than repeating explanations of all the charac-

ters here, labelled illustrations (Text-fig. 1) are provided for reference. These should suffice for all but a few terms, which are discussed below.

The "test" or "shell" of a cidaroid, strictly speaking, comprises the corona (comprising 20 vertical columns of plates, paired columns of ambulacral plates alternating with paired columns, A and B, of interambulacral plates) and plates of the upper apical system and periproct and of the lower peristomial system. Fossil tests almost always lack apical, periproctal and peristomial plates. Nevertheless, any such specimen is here referred to as a *test*, and the terms *apical system* and *peristome* refer to the openings where plates of these structures had been. As used here, *vertical diameter* of the test is the length of the axis from the border of the apical system to the border of the peristome. The *horizontal diameter*, as in other papers, is the diameter of the *ambitus* (the region of greatest horizontal circumference). Test plates near the apical system are here *adapical plates*, those near the peristome are *adoral plates*, and those at the ambitus, *ambital plates*.

Here, as in Mortensen (1928b, p. 9), the *interporiferous area* of the ambulacrum is the entire area between the poriferous zone of one ambulacral column and that of the adjacent column, but the numbers given in the measurement tables for the numbers of ambulacral tubercles (e.g., $M+1$) include only the *marginal tubercle* and the *inner tubercles* (those inside the marginals) on an individual ambulacral plate at the ambitus. Fossil cidaroid interambulacral plates often are disassociated from other test structures. Therefore, the term *median area* is applied throughout this paper to the area of individual interambulacral plates extending between the edge of the areole and the median suture, even for plates in intact tests, rather than the entire area between areoles of adjacent columns of interambulacral plates, as used in Mortensen.

Measurements and counts of test structures, where possible, have been taken at the ambitus. In each interambulacrum, only one plate, in one column or the other, is situated at the ambitus; in the adjoining column there are two plates, one slightly above and one slightly below the ambitus. Unless otherwise noted in the measurement tables, it is the single plate, in complete fossil interambulacra, or the nearest approximation in lesser fragments that has been used for interambulacral plate measurements and counts, and the am-

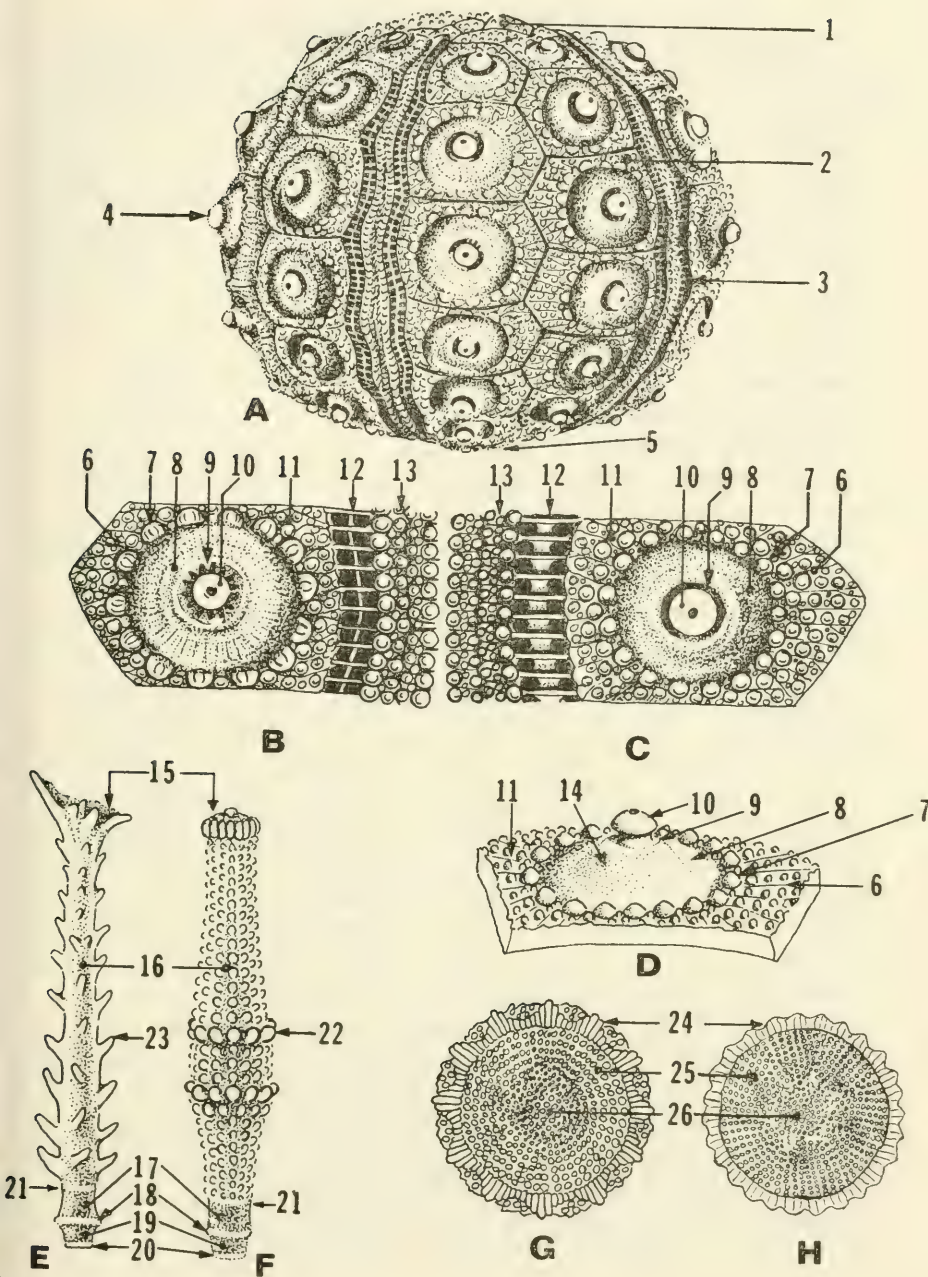
bulacral plates adjoining this interambulacral plate have been used for ambulacral measurements and counts.

Scattered among the *secondary tubercles* on both interambulacral and ambulacral plates are minute *miliary tubercles*, attachment points for pedicellariae. In this paper the *miliary tubercles* are rarely mentioned and are not represented in counts of tubercles.



Text-figure 1.—Morphological characters of cidaroids diagrammatically represented. **A**, test in side view; **B**, interambulacral plate with crenulate tubercle and ambulacral plates with nonconjugate pores, top view; **C**, interambulacral plate with smooth tubercle and ambulacral plates with conjugate pores, top view; **D**, interambulacral plate with smooth tubercle, oblique lateral view; **E**, spinulose radiole; **F**, nodulose radiole; **G**, transverse section of radiole, septa straight from cortex to core; **H**, transverse section of phyllacanthid-type radiole, septa arising in bundles.

- | | |
|--|---|
| 1. apical system opening | 13. interporiferous area of ambulacrum |
| 2. interambulacrum | 14. boss of primary tubercle |
| 3. ambulacrum | 15. tip of radiole |
| 4. ambitus | 16. shaft of radiole |
| 5. peristome (oral surface) | 17. collar of radiole |
| 6. median area of interambulacral plate | 18. milled ring of radiole |
| 7. scrobicular (secondary) tubercle | 19. base of radiole |
| 8. scrobicule of primary areole | 20. acetabulum of radiole |
| 9. platform of primary tubercle | 21. neck of radiole |
| 10. mamelon of primary tubercle | 22. whorls of large nodules |
| 11. adradial area of interambulacral plate | 23. spinule |
| 12. poriferous area of ambulacrum | 24. cortex of radiole |
| | 25. septal or lamellar layer of radiole |
| | 26. core or medulla of radiole |



ABBREVIATIONS OF TEST CHARACTERS

In tables of measurements of test characters in the "Systematics" section and in the Appendix, the following abbreviations are used:

AdrAW — adradial area width

AmPl — ambulacral plate

AmW — ambulacral width

ApSD — apical system diameter

ArW — areole width

Col — column

HD — horizontal diameter

IAmW — interambulacral width

IAmPl — interambulacral plate

IAmPlW — interambulacral plate width

IPorAW — interporiferous area width

IPorTub — interporiferous tubercles

MAW — median area width

PerD — peristome diameter

PorAW — poriferous area width

VD — vertical diameter

In cidaroids, each interambulacral plate bears a single large, primary spine. The term *radiole* is used here exclusively for this spine to distinguish it clearly from the *secondary spines*, those on areas of the plate outside the primary areole. The outer layer of the radiole, the *cortex*, is rarely smooth; it usually bears protuberances of one sort or another: rounded or peaked *nodules* or small to large thorns, here termed *spinules*. This ornamentation may be randomly scattered but commonly is in more or less distinct longitudinal series and may be joined into *ridges*. Ridges rarely are completely smooth. Those comprising peaked nodules joined at the base are here termed *dentate*, those with closely contiguous, rounded tubercles are *crenate*, and those with contiguous, distally inclined, small spinules are *serrate*. Both large and small nodules or spinules may occur on the same shaft, and in some genera the large protuberances may be grouped transversely or obliquely into *whorls*. The surface between and up the sides of the nodules, spinules or ridges rarely is completely smooth; usually, in living cidaroids, it is covered with

fine to coarse *hairs* that may be simple or anastomosed. In fossil radioles, minute nodules are commonly all that remains of the hairs.

On the adoral surface of the radioles of living cidaroids, the series of nodules, spinules, etc. commonly are narrower and more closely spaced. Isolated fossil cidaroid radioles also often have narrower, more closely spaced ornamentation on one surface, and that surface is here referred to as the adoral surface because there is no reason to suppose that fossil specimens are different in this respect from Recent specimens.

USEFULNESS OF CHARACTERS

Fossil cidaroids usually are found as fragments. Radioles rarely are adherent to or even closely associated with test specimens, prompting some workers to rely entirely on tests for systematic decisions. Yet, radiole specimens comprise the largest part of many collections of fossil cidaroids; for instance, there are over 20 times more specimens of radioles than of tests in the Caribbean collections considered in this paper. In many genera, radioles are more distinctive than tests. Assigning disassociated radioles and tests to a species, particularly when they are from the same collection site, or giving only a generic designation to radioles in the absence of test specimens is less likely to lead to inaccuracies in understanding the cidaroid fauna of an area than is treating radioles separately from the test specimens.

Most features of cidaroid radioles and tests are useful in making systematic decisions. Few of the features may be involved in establishing or confirming a taxon, but it is valuable to provide (as here) a more complete frame of reference against which others may compare similar specimens.

Certainly, variability and age changes are limitations to be taken into account, as has been recognized also by others (*e.g.*, Kongiel, 1937; Nestler, 1966). Growth of individuals involves not only increased dimensions but often changes in size relationships, as between the widths of areole, median area and adradial area of an interambulacral plate, and increase in numbers of certain structures such as test plates and series of protuberances on the radioles. All of these changes limit the classificatory value of many characters. The most reliable systematic decisions are based on series of test specimens (either whole tests or fragments that comprise an entire

interambulacrum and adjoining ambulacral plates), a good sample of radioles and pedicellariae, all collected from the same locality. Unfortunately, even excluding the pedicellariae, available specimens rarely meet these criteria.

The shape and type of ornamentation on the radioles and the nature of the ambulacral pores (except in *Cidaris*, *Calocidaris* and *Tretocidaris*) are two of the most useful characters for identifying cidaroids, because they are more or less independent of age of individuals. At least for the Cretaceous to Recent cidaroids, certain test characters that are "exceptions to the rule" (i.e., are found in only one or a small proportion of genera) also have value in assignment of even fragmental specimens to genus. Examples are deep crenulations completely encircling all or most of the primary tubercles (and acetabula of radioles from those tubercles) in both young and old specimens (e.g., *Histocidaris*, *Porocidaris*, *Acanthocidaris*), imperforate primary interambulacral tubercles (*Tylocidaris*, *Psychocidaris*), groove-like pores on the scrobicule of the primary interambulacral areole (*Porocidaris*), an unusually wide ambulacrum (*Centrocidaris*, some species of *Prionocidaris*), secondary interambulacral tubercles with attachment points for spines on the side rather than at the top of the tubercle (*Chondrocidaris*, *Actinocidaris*), two or more rudimentary primary interambulacral tubercles per column (*Stereocidaris*), distinct pits along sutures between plates (*Goniocidaris*, *Stereocidaris*), pits scattered all over the median and adradial areas of the interambulacral plates (*Temnocidaris*), and scrobicular tubercles no larger than other secondary tubercles on the interambulacral plates (*Rhyncocidaris* and the Subfamily Ctenocidarinae). Not all of these, however, are age independent and some, such as the stereocidarid rudimentary tubercles, are subject to misinterpretation.

In all cidaroids, interambulacral plates are added at the adapical margin of the test, alternately in columns A and B and in a regular sequence in the various interambulacra (Cutress, 1965). Early in the development of the plate, even after the radiole has begun to form, the areole appears rudimentary. Usually the new plate and its radiole are nearly completed before another plate begins to form in the same column, but as the cidaroid nears maximum size, development slows and there may be two plates per column carrying de-

veloping radioles. A few authors apparently have misinterpreted such developing plates as rudimentary plates.

In this study, specimens were separated into groups, using the characters mentioned above. The majority of such groups were referable to or similar to known Recent or fossil genera. Test measurements of specimens (arranged from large to small) in each group were tabulated, using the interambulacral plate width to determine the place of the fragmental specimens in the table if the horizontal diameter of the test could not be determined or estimated. If sizes and size relationships progressed in a smooth sequence, it seemed likely that the specimens all belonged to the same species. But discontinuities posed a problem: were these within permissible limits of variability for one species or were two or more species present? To help resolve this, tests of a number of Recent species, those believed closest to the Caribbean fossils, were measured.

Selected test data for Recent species studied are given in the Appendix. These data are arranged by size classes for each species because certain size relationships and counts change with growth. Ranges give an indication of variability within size classes, and the means show changes with age. The data were not processed further statistically for several reasons. Even though many specimens of Recent species were studied (15 measurements and counts for each specimen), most samples within size classes were too small to warrant sophisticated analyses, and the available fossil samples certainly were too small for meaningful statistics. The variability of most characters was clear enough from the tabulated data for this study, and the data in the tables could be used for comparative purposes without others having to treat their data statistically.

Some of the largest series of fossil test specimens to be separated to species in this study were referable to *Prionocidaris*. It is discouraging that the Recent species of this genus were among the most variable of those studied, particularly *Prionocidaris bispinosa* (Lamarck) and *Prionocidaris hawaiiensis* (A. Agassiz and H. L. Clark). Even excluding these two, a maximum spread of 12 to 18 per cent was found in characters that are expressed as percentages in the Appendix. For the two prionocidarids mentioned, the percentage spread was as high as 29 (ApSD/HD), 27 (PerD/HD) or 36 (VD/HD). In light of such variability in Recent species, caution

certainly is indicated in isolating as distinct taxa fossil specimens that present discontinuities in tabulated measurement series. On the other hand, specimens standing out in the series certainly can not be considered conspecific with other specimens in the series simply because they show no greater variability than Recent species, particularly if there are differences in two or more test characters. Radiole specimens from the same locality as a test are of considerable help in solving this problem.

Usefulness of radioles in separating genera and distinguishing species is considerable but not without limitations. Radiole shape may vary in different areas of the test. In some species the radioles are cylindrical or simply tapered at the ambitus but are fan-shaped, coronate, or cupulate on plates above the ambitus. Compared to ambital radioles, adoral radioles are always smaller and generally have less well-defined ornamentation on upper and lower surfaces. In some species, they have distinctly serrate lateral edges and may be flattened and curved. Radioles transitional in size and ornamentation between ambital and adradial radioles are present in most species. Radioles from the developing plates at the adapical margin of the test or regenerating radioles on other plates may be in all stages of development and until nearly completed (with hair coat in species where such is a feature) may appear different from ambital radioles. With experience it is possible to recognize developing, regenerating, transitional and adoral radioles and usually also adapical radioles. The latter three, if distinctive, may give important information as to genus or species, but it is the ambital radioles which provide the most reliable characters.

Usually the nature of the surface ornamentation of the ambital radioles is constant; for instance, if there are serrate ridges on ambital radioles of one specimen, there will be the same on other specimens of the same species. With growth of the cidaroid, the number of ridges on the radiole increases to a more or less constant maximum, but the size range of the protuberances or ridges stays more or less constant. The greatest variability in size and arrangement of the ornamentation is in the forms with spinulose radioles. For instance, in some of the fossil *Prionocidaris* species considered here, there apparently may be as many as three forms of radioles; some bear both distinct spinules and nodules, some are simply nodulose, and others are ridged.

Aside from ornamentation, shape of the ambital radioles is distinctive and therefore useful in some genera. Flattened radioles with serrate edges are typical of *Porocidaris*; small, beautifully fusiform radioles indicate *Tylocidaris*; long radioles that are triangular in cross-section and have smooth ridges and exceptionally long collars are typical in *Acanthocidaris*.

As Mortensen (1928b, p. 288) pointed out, the tests and radioles of Recent species of *Cidaris* and *Stylocidaris* are not sufficiently distinctive to serve alone in separating them to genus although the species can be identified with certainty by characters of the pedicellariae. Since pedicellariae are almost never found in the fossils, such forms (with nonconjugate pores, noncrenulate tubercles, and simply tapered, ridged radioles) have been referred by most workers to *Cidaris* or *Dorocidaris*. If use of *Cidaris* in this way is unavoidable, it should be noted as not being in the strict sense of the Recent genus.

SYSTEMATICS

Class ECHINOIDEA Leske

Order CIDAROIDA Claus

Family CIDARIDAE Gray

Subfamily HISTOCIDARINAE Mortensen

Genus HISTOCIDARIS Mortensen

Histocidaris sp. indet.

Plate 1, figure 1

Description. — Known specimens all fragments of very slender, cylindrical or slightly tapered radioles. Shaft of most fragments flattened on adoral surface and entirely smooth except for low, very sparse spinules on three to five microscopic, longitudinal ridges; all or all but one of ridges on adapical surface. Underlying fine septa visible through cortex. Five to six additional, very faint, smooth ridges on one fragment from locality 48; patches of minute surface irregularities, perhaps trabeculae of septal ridges, exposed through worn cortex on this and another fragment from same locality. In only known basal fragment, milled ring oblique, projecting, 1.9 times wider than proximal collar. Collar and base each with one side longer than other. Base 1.6 times as wide distally as proximally. Acetabulum scored by 12 distinct crenulations.

Discussion. — No fossil test specimens referable to *Histocidaris* were found in Miocene material examined. The Miocene radioles resemble those of Caribbean Eocene *Histocidaris sanchezi* (Lambert in Lambert and Thierry) but have fewer ridges with smaller and less projecting spinules, shorter collar, and more distinctly flattened adoral shaft surface. These differences and the considerable age difference indicate the Miocene and Eocene specimens do not represent the same species. In all the above-mentioned aspects, the Miocene radioles are more like those of the Recent Caribbean species *Histocidaris nuttingi* Mortensen. In fact, no real differences can be pointed out on the basis of these few specimens.

Two histocidarid tests were reported by Brito and Ramires (1974a, p. 267, pl. 1, figs. 2-3) from the lower Miocene Pirabas Formation of Brazil, but until the test of the Caribbean Miocene species is known, no meaningful comparisons are possible.

Several Oligocene and Miocene histocidarids reported from North Africa, Sicily and Italy appear, from descriptions and illustrations, to be similar to *Histocidaris* sp. indet.. These include *Cidaris vepres* Lambert (1931b, p. 74, pl. 3, fig. 22) and *Histocidaris oranensis* Lambert (1931b, p. 83, pl. 3, figs. 24-25).

Material. —

Locality	Catalogue Number	Collector	Number of radiole specimens
Bermúdez 48	PRI 29623	P. J. Bermúdez	3
Bermúdez 83	PRI 29624	P. J. Bermúdez	9
Bermúdez 229	PRI 29625	P. J. Bermúdez	3
Palmer 378	PRI 29626	R. H. Palmer	3

Stratigraphic occurrence and locality. — lower to middle (or possible upper) Miocene (Cojímar Formation), Cuba.

Measurements. — Basal fragment, 20 mm long, 1.5 mm wide, 1.3 mm thick; spinules 0.4-1 mm long, 0.3-0.4 mm wide, projecting (but worn) to 0.3 mm, and arranged in five sparse, longitudinal series; collar 2.7 mm long on one side, 3 mm on the other, 1.5 mm wide distally, 1.8 mm proximally; milled ring 3.4 mm wide; base 1.5 mm long on one side (same side as longest side of collar), 2.2 mm on other, 2.9 mm wide distally, 1.8 mm proximally; 12 crenulations around acetabulum.

Shaft fragments 5.5-18 mm long, 1.3-1.7 mm wide, 1.1-1.7 mm thick; spinules 0.5-1 mm long, 0.3-0.5 mm wide, projecting 0.2-0.4 mm, in three to five longitudinal series.

Histocidaris sanchezi (Lambert
in Lambert and Thiery)

Plate 1, figures 2-7

1925. *Rhabdocidaris sanchezi* Lambert in Lambert and Thiery, 1909-1925, p. 557 [footnote], pl. 14, figs. 1-3.
 1926. *Rhabdocidaris sanchezi* Lambert, Sánchez Roig, p. 29, pl. 2, figs. 1-3, pl. 3, fig. 4.
 1926. *Cidaris* sp., Sánchez Roig, p. 33, pl. 4, fig. 4.
 1931a. *Histocidaris sanchezi* (Lambert), Lambert, p. 300.
 1949. *Histocidaris sanchezi* (Lambert), Sánchez Roig, p. 23.

Description.—Test known only from detached plates; large, probably up to 60 mm in horizontal diameter (estimate based on comparison of plates of *H. sanchezi* with those of Recent histocidarids). Ambulacra slightly sinuate, about one-sixth width of interambulacra. Ten to 12 ambulacral plates adjoining known interambulacral plates (probably ambital), 15 to 16 per adapical interambulacral plate (most counts made from notches along adradial edges of plates). Pores oval, slightly oblique, depressed, nonconjugate, separated by thin wall, this bearing distinct knob on upper half in specimens examined [Sánchez Roig (1926, 1949) found no knob]. Ridges at top of plate raised and extending downward about half height of plate. Interporiferous area 1 to 1.2 times width of one poriferous area. Marginal tubercles about equal in size, filling most of interporiferous area; in specimens examined, area otherwise bare except for faint indications of very small tubercle below marginal on a few plates [Lambert (in Lambert and Thiery, 1909-1925, p. 557), reported a few tubercles inside marginals].

Number of interambulacral plates per column unknown. Areoles large, 66 to 75 per cent width of plate, only slightly depressed at upper margin but often sharply depressed toward lower margin. Median area narrow, less than one-fourth width of areole and only slightly wider than adradial area. Tubercle low; platform wide and deeply crenulate around entire circumference on ambital and adapical plates but crenulations less distinct on lower edge of some adoral plates. Scrobicular tubercles round, separated by ridge or small tubercle, lacking on lower margin of plates that apparently were situated at or below ambitus. Few small tubercles outside scrobicular ring. Narrow bare area adjoining slightly depressed median suture.

Ambital radioles apparently (from known fragments) long, slender, cylindrical, sometimes distinctly curved. Tips unknown. Eight to 20 distinct cortical ridges on shaft, one-half or fewer bear-

ing large, sparse, distally inclined spinules on proximal two-thirds, otherwise smooth. Spinules typically uniform in size on different surfaces of any one radiole (*i.e.*, no distinct adoral surface), some projecting 2 to 9 mm; tips of spinules simple. Shaft otherwise completely smooth; shiny in well-preserved specimens. Septa of underlying layer often visible through thin cortex. No distinct neck. Collar long, either about same width throughout or proximally widened to as much as 1.6 times distal width. Milled ring prominent, somewhat oblique, 1.2 to 1.5 times width of proximal end of collar (Table 3). Base averaging 1.5 times wider distally than proximally. Acetabulum with 12 to 13 deep crenulations.

One known fragment (SUPTC 10240 from Palmer loc. 1030), apparently from transitional or oral radiole, with only lateral series of spinules.

Discussion. — Some of the interambulacral plates collected by Palmer and Bermúdez are nearly identical to the one pictured by Lambert (*in* Lambert and Thiery, 1909-1925, pl. 14, fig. 3). Sánchez Roig (1926, p. 29) did not find a nodule between the pores on ambulacral plates of his specimens whereas there are distinct knobs in the Palmer and Bermúdez material. It may be that Sánchez Roig's specimens were weathered and the knobs had disappeared.

There are some discrepancies between the Palmer and Bermúdez radiole fragments and the Lambert illustrations and description. Lambert may have had only photographs of Sánchez Roig's specimens on which to base his description, for Sánchez Roig, apparently with specimens in hand, provided a description without these points of difference. The maximum width of a radiole estimated to have been about 120 mm long was given as 4 mm by Lambert but 3 mm by Sánchez Roig, the latter within the range of widths of Palmer and Bermúdez material. Lambert said the collar is short; Sánchez Roig did not mention length of collar, indicating only that the spinules begin 20 to 30 mm from the base of the radiole. Tips of spinules on the lower portion of the radiole shaft are sometimes bifid according to Lambert but not mentioned at all by Sánchez Roig. There are no bifid spinules in Palmer and Bermúdez specimens although rarely bases of the spinules are contiguous or, in the ANSP and SUPTC specimens, some tips are broken unevenly. If Lambert's figures were prepared from photographs by an artist not familiar with the speci-

mens, it would be understandable how a misinterpretation of both spinules and collars could occur, because the distal limits of the latter are often indistinct in photographs.

The Eocene species *Histocidaris sanchezi* resembles two Caribbean species, *Histocidaris nuttingi* Mortensen and *Histocidaris* sp. indet., Recent and Miocene, respectively, and probably is their ancestor. Differences between *H. sanchezi* and *H.* sp. indet. were detailed on previous pages. From *H. nuttingi*, *H. sanchezi* differs in having fewer tubercles on the ambulacral plates (perhaps because extant plates are from above the ambitus) and on the median area of interambulacral plates, a larger maximum number of ridges on the radioles (13 is apparently the maximum in *H. nuttingi*, three to six of which bear spinules), larger spinules (they rarely project as much as 1.5 mm in *H. nuttingi*), and longer collars (they are commonly less than 6 mm long in *H. nuttingi*).

H. sanchezi may have been a deep-water species; Recent histocidarids are found at depths of from 200 to 1440 m.

A holotype was not designated by Lambert (*in* Lambert and Thiery, 1909-1925). Sánchez Roig mentioned "Tipo No. 106, Colección Sánchez Roig" in his 1926 paper and "Tipo No. 506" in 1949 but in neither paper did he indicate which specimen was the holotype. None of the Sánchez Roig specimens was seen.

Material.—

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez (a)	PRI 29627	P. Bermúdez	—	3
Bermúdez 261	PRI 29628	P. Bermúdez	—	3
Palmer 942*	ANSP 16843	R. H. Palmer	—	2
Palmer 942*	LSJU 53242	R. H. Palmer	1	2
Palmer 942*	PRI 29629	R. H. Palmer	48	7
Palmer 942*	SUPTC 10239	R. H. Palmer	4	8
Palmer 942*	PRI 29630	P. Bermúdez	—	2
Palmer 1030	PRI 29631	R. H. Palmer	—	6
Palmer 1030	LSJU 53243	R. H. Palmer	—	9
Palmer 1030	SUPTC 10240	R. H. Palmer	—	12
Palmer 1102	LSJU 53241	R. H. Palmer	1	1

* = equivalent of type-locality.

Stratigraphic occurrence and locality.—lowest Eocene, middle Eocene (Loma Candela Formation) and upper Eocene (Consuelo Formation), Cuba. The type-locality was indicated as Miocene by Lambert (*in* Lambert and Thiery, 1909-1925, p. 557) and Sánchez Roig (1926, p. 30), as lower Eocene by Sánchez Roig (1949, p. 23), and as late Eocene by Palmer (1948, p. 58) and here.

Measurements. — See Table 1 for dimensions of interambulacral plates from the type-locality and its equivalent (Palmer loc. 942). See Table 2 for dimensions of basal ends of radioles.

Table 1. — Measurements of *Histocidaris sanchezi* interambulacral plates thought to have had near-ambital position.

Characters	Lambert specimen*	SUPTC 10239	PRI 29629	PRI 29629	PRI 29629
IAmPIW (mm)	17	18	16.5	16	16
ArW (mm)	12	13	11	11.5	10.5
MAW (mm)	3	3	3	2.5	3
AdrAW (mm)	2	2	2.5	2	2.5
ArW/IAmPIW (%)	70	72	67	72	66
MAW/IAmPIW (%)	18	17	18	16	19
AdrAW/IAmPIW (%)	12	11	15	12.5	16

* = measurements taken from Lambert and Thierry, 1909-1925, pl. 14, fig. 3.

Ambulacral plates were found adjoining very few, and only adapical, interambulacral plates in material examined; in those, PorAW 1 mm, IPorAW (per plate) 0.7 mm in one fragment; in another, PorAW 1 mm, IPorAW 0.9 mm.

Radioles: maximum length 120 mm, width 4 mm, according to Lambert. Longest fragment examined (ANSP 16843, in two parts): 113 mm long, 3.8 mm wide; widths of other radiole fragments 2-3.5 mm. Largest spinules 1.5 mm wide, 3.2 mm long through base, projecting as much as 2.9 mm. For dimensions of basal ends of radioles, see Table 2.

Table 2. — Dimensions, in mm, of basal ends of radioles of *Histocidaris sanchezi*.

Maximum width shaft	Length collar*	Distal/proximal width collar	Width milled ring	Length base*	Distal/proximal width base
3.5	6.0	3.4/5.7	6.4	2.2	5.1/3.5
3.2	5.3/5.6	3.2/5.0	5.8	2.6/2.4	4.8/3.7
2.5	6.4/6.7	2.5/4.0	4.7	—	4.5/2.6
2.4	6.1/6.7	2.4/3.4	4.6	2.9/1.9	4.0/2.6
2.0	7.2/7.7	2.0/2.6	4.0	2.4/2.1	3.5/2.1

* = paired values reflect measurements on opposite sides of collar and base.

Subfamily STEREOCIDARINAE Lambert

Genus STEREOCIDARIS Pomel

Stereocidaris sp. A

Plate 1, figures 8, 9

Description. — Four known specimens: broken, isolated interambulacral plates and small pieces of ambulacrum worn smooth

except for pore slits. Interambulacral plates and areoles apparently about as wide as high. Scrobicular tubercles moderately prominent; crowded, small tubercles outside scrobicular ring.

Extant fragments indicate radioles were slightly tapered, up to 50 mm or more long, to 3.6 mm wide, commonly slightly compressed (approx. 1.5 to 2 mm difference between maximum and minimum diameters). Shaft having 11 to 17 longitudinal, serrate or (when worn) crenate ridges; minute granules (hair coat remnants?) in grooves between ridges on some fragments. Collar short to moderately long, slightly wider proximally than distally. Milled ring worn on known specimens but apparently only slightly wider than proximal collar. Base usually shorter than collar and 1.2 to 1.5 times as wide distally as proximally. Acetabulum worn in most specimens but may have faint crenulations on one side in two specimens.

Discussion. — The known test fragments alone do not especially indicate *Stereocidaris*, but radiole fragments collected at the same locality are stereocidarid in appearance and are similar to others listed below under "Material."

Stereocidaris ingolfiana Mortensen, which lives now in the Caribbean, may represent the present continuation of a lineage that included *S. sp. A* and that became established in the Caribbean as early as the Cretaceous. One difficulty with such an hypothesis is the lack of any indication of "wings" on the Caribbean fossil radioles thought to be stereocidarid; an extra-wide ridge would remain even if the "wing" were eroded. The projecting ridge could be a late development. At least one Cretaceous species that appears to be stereocidarid and is known from the Mediterranean area apparently had radioles with one higher and wider ridge: *Cidaris angulata* Peron and Gauthier (*in* Cotteau, Peron and Gauthier, 1879, p. 178, pl. 13, figs. 13-16) from the Cenomanian of Algeria, known only from radioles but perhaps conspecific with *Cidaris atrophæa* Peron and Gauthier (*in* Cotteau, Peron and Gauthier, 1879, p. 177, pl. 19, figs. 7-12) from the same locality, known only from a test that is distinctly stereocidarid. On the other hand, no references were found to stereocidarid radioles with one wide ridge from Eocene or younger strata in the Mediterranean area.

Material. —

Locality	Catalogue Number	Collector	Number of radiole specimens
Palmer 1081	PRI 29739	R. H. Palmer	2
Palmer 1085	CASGTC 58721	R. H. Palmer	5
Palmer 1085	LSJU 53260	R. H. Palmer	41
Palmer 1085	PRI 29688	R. H. Palmer	110

Stratigraphic occurrence and locality. — middle Eocene and upper Eocene (San Luis Formation), Cuba.

Measurements. — Radioles: estimated maximum length at least 50 mm; width of shaft usually 2.4-3 mm (range 1.5-3.6 mm); ridges usually 0.3-0.5 mm wide (range 0.2-0.6 mm); minute nodules (remnants of hairs?) about 0.04 mm in diameter; collars 0.7-1.6 mm long on six of nine basal fragments, 1.8-2.6 mm long on other three fragments; collar 1.2 times as wide proximally as distally; milled ring 0.05-0.25 mm wider than proximal end of collar; base 0.7-0.9 mm long in four of seven specimens, 1-1.25 mm long in the other three, with a proximal width 1.2-1.5 times less than distal width.

Stereocidaris sp. B

Plate 1, figures 10-13

Description. — Test known only from few, incomplete, worn, interambulacral plates, these almost as high as wide and well tuberculated. Areoles large (63 to 71 per cent width of plate in two best preserved specimens), considerably depressed. Tubercles large, moderately high, smooth, perforate. Scrobicular tubercles prominent, separated by small tubercle or ridge. Narrow median and adradial areas covered otherwise to sutures with small, crowded tubercles. Corners of plates incurved so median suture probably depressed.

Radiole fragments up to 5.7 mm wide, from radioles apparently up to 40 mm long, either columnar or fusiform. Tips obtuse, prominently grooved, some with simple, low spinule or V-shaped prominence at end (*not* eucidarid rosette). Shaft with 11 to 23 crenate to smooth, longitudinal ridges, these commonly fewer and more prominent distally and narrower and more closely spaced on adoral surface. Surface between and up sides of ridges covered with minute nodules 0.04 to 0.15 mm in diameter. Neck, visible on some fragments, slightly longer than collar. Known collars 1.9 mm long or shorter, distinctly widened proximally. Milled ring about 1 mm wider than proximal end of collar; grooves of ring extending part-way down base in some specimens. Base about same length as collar,

up to 1.5 times wider distally than proximally. Acetabulum usually smooth but in some specimens having faint crenulations along one side.

Discussion. — Several specimens in lot PRI 29737 from Palmer locality 115 and one in SUPTC 10247 from Palmer locality 757 have sharply peaked nodules or low spinules rather than ridges. These protuberances are 0.2 to 0.5 mm wide and project up to 0.5 mm. They are lumped here with the other specimens of this indeterminate species but with some reservations.

The Cuban test fragments, especially the interambulacral plate (CASGTC 58720) from Palmer locality 832, and the radioles resemble those of Recent stereocidarids.

There are definite similarities between test specimens of *S. sp. B* and those of *Cidaris texanus* W. B. Clark (1891, p. 751; 1893, p. 36, pl. 7, figs. 1a-e), which Clark recorded from the Washita group of the Comanche series (upper Albian or lower Cenomanian) of Texas but which Cooke (1953, p. 5) said occurs instead in the Austin chalk (Coniacian-Santonian) and Anacacho limestone (Campanian). Test specimens of *S. sp. B* also are similar to those of *Cidaris splendens* (Morton) and *Cidaris sp. aff. C. splendens* (Morton) from the Paleocene of Alabama and New Jersey, as illustrated by Cooke (1959, pl. 1, figs. 10-11). However, the known Caribbean material is too fragmentary to assign at this time to either of those species. Also, Clark (1893, p. 37) described *C. texanus* as having radially ridged interambulacral areoles, and this is not true of the areoles on Cuban specimens.

As discussed under *Stereocidaris?* sp. C., there apparently were stereocidarids in South America and Mexico during the Early Cretaceous. *S. sp. B* may have been a descendant of one of them, or it may have derived from a European species such as *Cidaris subvesiculosa* d'Orbigny from the Senonian of France and England (Cotteau in d'Orbigny, 1862-1867, p. 257, pls. 1059-1061).

The two Jamaican Late Cretaceous radiole fragments (USNM 232519) included questionably with the Cuban material in the "Material" list below have new ridges forming between older ridges. Although they are much like two fragments (PRI 29699) from Palmer locality 895P in Cuba that were collected along with a worn but stereocidarid type of interambulacral plate, there are too few

Jamaican radioles to place much confidence in their referral to any species.

The Brown test fragment, also questionably referred to the species, is from Guatemala. It is very worn but shows sinuous ambulacra, a distinctly depressed poriferous zone, nonconjugate pores, and high interambulacral plates, all features typical of sterocidarid tests.

Material. —

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez (c)	PRI 29691	P. J. Bermúdez	—	4
Bermúdez (d)	PRI 29692	P. J. Bermúdez	—	57
Bermúdez (e)	PRI 29762	P. J. Bermúdez	—	1
Bermúdez 26	PRI 29758	P. J. Bermúdez	—	1
Bermúdez 76A	PRI 29690	P. J. Bermúdez	—	7
Bermúdez 148	PRI 29689	P. J. Bermúdez	—	1
Bermúdez 400	PRI 29761	P. J. Bermúdez	—	2
Brown (a)	?USNM 243089	Barnum Brown	1	—
Palmer 115	PRI 29693	R. H. Palmer	—	37
Palmer 115	PRI 29737	R. H. Palmer	—	9
Palmer 757	SUPTC 10247	R. H. Palmer	—	8
Palmer 757	LSJU 53261	R. H. Palmer	—	7
Palmer 812	PRI 29694	R. H. Palmer	—	32
Palmer 812	CASGTC 58719	R. H. Palmer	—	8
Palmer 832	CASGTC 58720	R. H. Palmer	1	—
Palmer 832	LSJU 53262	R. H. Palmer	—	2
Palmer 832	PRI 29695	R. H. Palmer	1	34
Palmer 835	PRI 29696	R. H. Palmer	5	5
Palmer 888	PRI 29697	R. H. Palmer	—	19
Palmer 894	PRI 29698	R. H. Palmer	2	13
Palmer 895P	PRI 29699	R. H. Palmer	1	15
Palmer 895P	LSJU 53263	R. H. Palmer	—	2
Palmer 1245	PRI 29738	R. H. Palmer	—	6
USGS 29956	?USNM 232519	N. D. Sohl <i>et al.</i>	—	2

? = questionably referred to species.

Stratigraphic occurrence and localities. — Upper Cretaceous (most localities in Habana Formation, some in Big Boulder Bed Member) and apparently also Paleocene (Madruga Formation), Cuba. Possible Upper Cretaceous (Maestrichtian), Jamaica.

Measurements. — Interambulacral plate from Palmer locality 895P (PRI 29699): IAmPIW and height 11.7×9.1 mm; ArW and height 8.3 mm (71% IAmPIW) $\times$ 7.5 mm; MAW 1.8 mm (15% IAmPIW); AdrAW 1.8 mm. Interambulacral plate from Palmer locality 832 (CASGTC 58720): IAmPIW and height 9.9×9.8 mm; ArW and height 6.2 mm (63% IAmPIW) $\times$ 6.2 mm; MAW 2.4 mm (24% IAmPIW); AdrAW 1.9 mm.

Radiole fragments: 2-5.7 mm wide; ridges 0.25-0.6 mm wide and spaced 0.3-1.2 mm apart transversely on adapical and lateral surfaces, somewhat narrower and more closely spaced on adoral surface; minute nodules (remnants of hair coat?) 0.04 mm and (or) 0.08-0.15 mm wide; collars 0.6-1.9 mm long, 1.02-1.2 times as wide proximally as distally, milled ring only slightly wider than proximal end of collar; bases 0.7-1.7 mm long; width 1.3-1.7 times less proximally than distally.

Stereocidaris? sp. C

1957. *Cidaris* sp. Osten, p. 578, pl. 63, fig. 4.

Discussion. — Osten (1957) mentioned a radiole tip collected from the Morro Blanco Member of the Barranquín Formation, Venezuela. From the illustration, this specimen is similar to tips of Cuban stereocidarid radioles although the latter were found in Late Cretaceous strata. He also mentioned the similarity of his specimen to the radiole tip, from the Lower Cretaceous (Quarry limestone) of Texas, illustrated by Adkins and Winton (1920, pl. 9, fig. 5). The latter also resembles radioles of *Stereocidaris*.

Osten found that although the Barranquín Formation contained North American elements present in the Glen Rose and associated formations of Albian age, it also had European elements of Neocomian or Barremian age. He concluded the Barranquín - Glen Rose relationship was one of facies only, that the Barranquín was probably of Neocomian age, and that the Early Cretaceous faunas of Venezuela, Mexico and Texas probably spread from the Caribbean - Gulf of Mexico basin in succeeding stages during transgressions of continental borders.

Cidaris mullerriedi Lambert (1935, p. 365, pl. 16, figs. 13-14) from the Aptian of Mexico appears from illustrations to be much like the Late Cretaceous species *Cidaris texanus* (mentioned here under *Stereocidaris* sp. B), and both of these species resemble some of the tests of *Stereocidaris branneri* White (1887, p. 247, pl. 28, figs. 2-3) from the Riachuelo Formation, Maruim Member (Middle Albian), Sergipe, Brazil.

As discussed in the "Synthesis" section, consideration of *S. branneri* in the ancestry of any Caribbean or Gulf area species may require a dispersal route south from Sergipe, around the southern

tip of South America and then northward. Yet, it should not be discounted because of this. Maury (1936, p. 261) and Brito and Ramires (1974b, p. 276) also allied *C. texanus* with *S. branneri*. A new Caribbean phyllacanthid species (to be mentioned later) may be allied to another species from the Riachuelo Formation in Brazil. Therefore, connections between Sergipe and the Caribbean - Gulf area may have been easier than Albian paleogeography, as presently understood, would suggest, and *S. branneri* may, in fact, have reached the Caribbean area and have been part of the stereocidarid lineage that included *Stereocidaris* spp. A and B. Because of this, I have included here a more complete description and measurements of White's four most complete specimens of *S. branneri*.

Description of *Stereocidaris branneri* (White)

(Measurements of test specimens given in Table 3)

Ambulacra sinuate. Poriferous areas distinctly depressed. Pores separated by wall one pore width wide or slightly wider; groove at lower edge of plate narrow in small specimens but sufficiently wide in largest specimen that pores appear subconjugate. Marginal tubercles contiguous and in regular series; one to four inner tubercles equal or nearly equal in size to marginals.

In largest specimens, two plates per column with rudimentary tubercles; in other specimens, only plates with imperforate, incomplete tubercles are those (no more than one per column) newly added at apical margin. All areoles separated by at least a double row of scrobicular tubercles. Primary tubercles moderately high; platform smooth. Scrobicular tubercles round to oval; inner edge sloping to scrobicule. In some specimens, particularly from largest individuals, scrobicular ring raised into "lip" around primary areole. Surface of plate otherwise covered to sutures with crowded smaller but about equal-sized tubercles. Horizontal as well as median sutures distinctly depressed; edges of plates sloping steeply away from scrobicular ring. Some specimens with distinct pits in horizontal and median sutures.

No radioles were associated with White's specimens; however, Brito and Ramires (1974b, pl. 2, fig. 2) illustrated a robust radiole about 36 mm long and 5.6 mm wide.

Table 3.—Measurements of most complete of examined tests of *Stereocidaris branneri*.

Characters (in mm)	USNM 243091a	USNM 243090	USNM 243092	USNM 243091b
HD	65.	60	50.	41
VD	—	42	35.	31
PerD	—	24.5	—	17
ApSD	21.5	22	—	14
IAmW	32	31	—	21
AmW	6.5	5	5.5	6
IAmPIW	19.5	18	16	12
ArW	9	8.5	8.5	6.5
MAW	7.5	6.5	5	3.5
AdrAW	3	3	2.5	2
PorAW	1.5	1.5	—	2
IPorAW	3.5	2	—	3
(as percentages)				
VD/HD	—	70	70.	75
AmW/IAmW	20	16	—	29
ArW/IAmPIW	46	47	53	48
MAW/IAmPIW	38	35	31	35
(as numbers)				
IAmPl:Col	—	6-7	—	6-7
AmPl:IAmPl	24-25	19-20	25-26	19-23
IPorTub:AmPl	M+3-4	M+1-2	M+1-2	M+2

. = estimate.

Subfamily **CIDARINAE** GrayGenus **CIDARIS** Leske**Cidaris bermudezi**, new species

Plate 2, figures 2-8

1922. *Cidarid* sp. a, Jackson, p. 18, fig. 1.1963. ?*Cidarid* sp., Gordon, p. 631.

Diagnosis. — Test small; pores nonconjugate; ambulacra nearly straight, 30 per cent or more the interambulacral width; areoles large, more than 65 per cent of plate width. Radioles 2 mm wide or less; with 10 to 14 more or less uniformly serrate (or crenate if worn) ridges; collar 1.5 mm long or less, slightly wider proximally than distally.

*Description**. — Known test fragments from small to medium-sized individuals, largest probably no more than 35 mm in horizontal diameter. Ambulacra nearly straight, about one-third width of interambulacra or slightly wider. Six ambulacral plates per inter-

*of Cuban specimens on which the species is based. Description of questionably conspecific Puerto Rican material follows.

ambulacral plate at ambitus in most complete specimen (from very small test), 11 and 13 adjoining two isolated, obviously adapical plates from larger test. Pores in smallest specimen oval, slightly oblique; wall about one pore width wide, high, in some plates bearing knob on upper part but grooved along lower edge. Interporiferous area about 1.2 to 1.5 times as wide as one poriferous area; completely filled by marginal tubercles in fragments from smallest specimen but having additional, small tubercles near bottom of plate in fragments from larger individuals.

Five to six interambulacral plates per column in smallest specimen; number in large individuals unknown. Areoles large, 66 to 73 per cent width of plate, very slightly or not depressed. At least a few scrobicular tubercles at horizontal sutures of known interambulacral plates. Primary tubercles large, smooth, all perforate except several adoral, apparently incompletely developed, imperforate tubercles on smallest specimen. Scrobicular tubercles round, separated by small tubercle or ridge. Median and adradial areas almost completely filled by scrobicular tubercles, or having very few, small, outer tubercles.

Radiole fragments, thought to belong to same species, from long, slender, slightly tapered radioles. Tips unknown. Shafts with up to 14 serrate or crenate ridges, these of equal width on all surfaces of one specimen. Minute granules (hair coat remnants?) between ridges on widest fragment. Short neck visible on several specimens. Collars on known fragments up to 1.5 mm long, slightly widened toward inconspicuous milled ring. Bases shorter; acetabula apparently smooth.

*Description**. — One fragment (AMNH 18566) from southern part of Puerto Rico, 2 mm wide but with no more than 10 crenate ridges. Other radiole fragments and a test fragment (PRI 29753), taken from a small block of limestone at a collection site in northern part of island. Radioles with 16 to 24 ridges bearing low serrations; minute granules (remnants of hairs?) between and up sides of serrations; only known tip slightly widened, oblique, rimmed by ridges and excavate into a "hoof." In fragment comprising an adapical interambulacral plate with adjoining ambulacrals, ambulacrum

*of Puerto Rican specimens that may not be conspecific with those from Cuba described above.

slightly sinuate. Pores oval, subconjugate, separated by wall slightly more than one pore width wide, raised on upper part but depressed along bottom of plate. Marginal tubercles in regular series, bases contiguous; one or two small, inner tubercles. Scrobicular tubercles nearly round, separated by small tubercle. Plates otherwise covered to sutures with few, small tubercles.

Discussion. — As indicated by Mortensen (1928b, p. 288), in the absence of pedicellariae it is not possible to distinguish the genera *Cidaris* and *Stylocidaris*, and it has long been the practice to use *Cidaris* in a broad sense for fossil forms that appear to belong to one or the other genus. *Cidaris* is here designated in this imprecise sense.

In Recent species of *Cidaris* and *Stylocidaris*, an ambulacral width 30 per cent or more of interambulacral width, as in *C. bermudezi*, is the exception (see Appendix). It is the genera with conjugate pores that typically have wide ambulacra. In the holotype of *C. bermudezi* and other material referable to that species, the wall between the pores is raised except on the lower part of the plate. Comparisons of ambulacral plates in the fossils with those in Recent specimens of comparable size (determined by widths of adjoining interambulacral plates) show it is a marked difference in the width of the poriferous area, more specifically of the wall between the pores, that accounts for the difference in ambulacral width. A similar difference between fossil and Recent species exists in *Calocidaris* and *Tretocidaris*.

There are no flattened fragments among the Cuban radioles, indicating that *C. bermudezi* may not be a link between Eocene *Cidaris cubensis* Lambert (discussed below) and the Recent Caribbean species *Cidaris blakei* A. Agassiz.

The radiole fragment from southern Puerto Rico is wider than any of the Cuban fragments and so would be expected to have more longitudinal serrate ridges but in fact has fewer. This may belong to a different species. Some of the northern Puerto Rican radiole fragments are as slender as the Cuban radioles but have more longitudinal ridges. These may represent still another species. The large number of ridges (up to 24) and the "hoof" tip suggest that this form may be an ancestor of Recent *Cidaris abyssicola* (A. Agassiz). More material will be needed to determine if the Puerto Rican specimens are truly distinct from Cuban *C. bermudezi*.

Gordon (1963, p. 631) mentioned briefly (as *Cidaris* sp.) but did not illustrate parts of three or four weathered, recrystallized tests and an unstated number of *Cidaris* radioles from the Miocene of Mona Island and Puerto Rico. I have not seen these specimens. As far as can be determined from records and specimens, no *Cidaris* species was present in the southeastern United States in the Miocene.

Cidaris bermudezi is named for Dr. Pedro J. Bermúdez who collected many of the known specimens.

Holotype. — PRI 29603, a test fragment collected by Dr. P. J. Bermúdez at Bermúdez locality 234, Habana Province, Cuba.

Paratypes. — PRI 29600-29602, 29064, 29605-29607, 29745, 29751.

Material. —

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez 83	PRI 29600	P. J. Bermúdez	—	4
Bermúdez 229	PRI 29601	P. J. Bermúdez	—	10
Bermúdez 230	PRI 29602	P. J. Bermúdez	4	1
Bermúdez 234	PRI 29603	P. J. Bermúdez	1*	—
Bermúdez 234	PRI 29604	P. J. Bermúdez	4	9
Cutress 1	?PRI 29753	B. Cutress	1	10
NYAS-AMNH 195	?AMNH 18566	C. A. Reeds	—	1
Palmer 1018	PRI 29605	R. H. Palmer	3	10
Palmer 1025	PRI 29606	R. H. Palmer	2	1
Palmer 1026	PRI 29607	R. H. Palmer	—	18
Palmer 1026	PRI 29745	R. H. Palmer	—	8
Palmer 1026	PRI 29751	P. J. Bermúdez	—	1

? = questionably referred to species; * = holotype.

Stratigraphic occurrence and localities. — lower to middle (and possibly upper) Miocene (Cojímar Formation) and middle Miocene (Güines Formation, Basal Yumurí limestones), Cuba. Specimens from Oligocene to lower Miocene (Lares Formation), northwestern Puerto Rico, and Oligocene (Juana Díaz Formation), southwestern Puerto Rico, questionably referred to species.

Measurements. — See Table 4 for test measurements.

Radioles. — Cuban fragments 1-1.5 mm wide, with 10 to 14 ridges up to 0.25 mm wide and spaced 0.23-0.37 mm apart transversely. Neck to 1 mm long on a few; collars 1-1.5 mm long and not more than 0.5 mm wider proximally than distally; milled ring about 0.5 mm wider than proximal end of collar; base up to 1 mm long and 1.3 times wider distally than proximally.

Fragment from southern Puerto Rico, 1.75 mm long, 2 mm wide,

Table 4. — Measurements of tests of *Cidaris bermudezi* n. sp.

Characters	PRI 29753	PRI 29603 (holotype)	PRI 29605	PRI 29602
(in mm)				
HD	—	—	—	8-10.
VD	—	—	—	6.
PerD	—	—	—	—
ApSD	—	—	—	—
IAmW	13.	9.1.	8.8.	3.5
AmW	4.4	3	2.7.	1.3
IAmPlW	7.	5	4.6	2.2
ArW	4	3.3	3.2	1.5
MAW	2	1	0.9	0.4
AdrAW	1	0.7	0.6	0.3
PorAW	1	0.9	0.8	0.35
IPorAW	1.2	1.2	1.1	0.55
(as percentages)				
VD/HD	—	—	—	60-75.
AmW/IAmW	35.	33.	31.	37
ArW/IAmPlW	57	66	70	68
MAW/IAmPlW	29	20	20	18
(as numbers)				
IAmPl:Col	—	—	—	5-6
AmPl:IAmPl	13.	13	11	6
IPorTub:AmPl	M+1	M+0-1	—	M+0

. = estimate. PRI 29753 may belong to a separate species.

with eight to 10 low crenate ridges 0.25 mm wide and spaced 0.5 mm apart.

Fragments from northern Puerto Rico, 12 mm or less in length, 1.2-2.5 mm wide, with 16 to 24 low serrate ridges 0.1-0.35 mm wide and spaced 0.1-0.3 mm apart. Neck 1.5 mm long; collar 2 mm long, 2.4 mm wide distally, 2.7 mm proximally; milled ring 2.9 mm wide; base 1.3 mm long, 2.7 mm wide distally, 2 mm proximally.

Cidaris cubensis Lambert in Lambert and Thiery

Plate 2, figure 1

1925. *Cidaris cubensis* Lambert in Lambert and Thiery, 1909-1925, p. 558 [footnote], pl. 14, figs. 4-5.

1926. *Cidaris cubensis* Lambert, Sánchez Roig, p. 31, pl. 3, figs. 1-2, pl. 2, fig. 4.

1949. *Cidaris cubensis* Lambert, Sánchez Roig, p. 24.

Description. — Test unknown. Holotype, described by Lambert, radiole fragment apparently from very young individual, 24 mm long, 0.5 mm at widest, with 10 longitudinal ridges bearing small granules, intervals between ridges smooth and wider than ridges, collar short, milled ring projecting and broadly grooved, articular surface smooth.

In fragments from larger radioles, collected by Palmer apparently at type-locality, shafts cylindrical, 2.8 mm wide or narrower, having up to 16 finely serrate, longitudinal ridges. Surface between and up sides of ridges covered with very narrow, minutely serrate ridges, apparently extensions of septa. Two tips greatly flattened and widened into blades. Collar of only basal fragment not quite 2 mm long, scarcely widened proximally; milled ring and base missing.

Discussion.—The holotype is too small to show significant features other than serrate ridges. Even the number of ridges can not be considered characteristic of the species inasmuch as the number increases with growth of a radiole. Alone this specimen is a poor basis for the species. However, the serrate radioles collected by Palmer at the type-locality probably belong to the same species and can be considered topotypes.

C. cubensis is distinguished from the Miocene species *Cidaris bermudezi* n. sp. by its greater age and broad, flattened radiole tips.

As in *C. bermudezi*, use of the genus *Cidaris* here is not in *sensu stricto*. However, the bladelike tips of its radioles are an indication that *C. cubensis* may be a true *Cidaris*.

Although flattened tips are unknown from the Caribbean Oligocene or Miocene, *C. cubensis* may be the ancestor of the Recent Caribbean species *Cidaris blakei*, which often bears fan-shaped radioles. Maximum widths of the flattened tips and of the shafts in *C. blakei* are greater than those in *C. cubensis*, and the serrations in *C. blakei* radioles are commonly more discrete. Otherwise, the radioles of the two species are much alike.

On the other hand, *C. cubensis* may have died out in the Caribbean, and the ancestor of *C. blakei* may have lived in the Tethys. Fossil fan-shaped radioles from the Mediterranean area have been mentioned by several authors: unnamed radioles that Simonelli (1896, p. 257) and Del Bue (1900, p. 129) believed were similar to radioles of *C. blakei* but did not figure; *Rabdocidaris* [*sic*] *oxyrinae* Meneghini (Meneghini, 1862, p. 13, pl. 2, figs. 3) and radioles and plates of *Dorocidaris* cf. *blakei* A. Agassiz, mentioned by Vinassa de Regny (1897, p. 146), all from the Miocene or Pliocene of Italy; and *Cidaris sahelensis* Pomel (Pomel, 1887, p. 324, pl. 1, figs. 1, 20; Cotteau, Peron and Gauthier, 1891, p. 239, pl. 1, figs. 1-20) from the Pliocene of Algeria, a synonym of *C. oxyrinae* according to Airaghi (1901, p. 167).

At least one species with fan-shaped radioles was present in the Mediterranean area during the Eocene. *Rabdocardaris* [sic] *rosavendai* Airaghi (Airaghi, 1901, p. 171, pl. 19, figs. 34-40) from the late Eocene of Italy had radioles similar to those of *C. blakei*, according to Airaghi, although they differed in their greater size and thickness and finer ornamentation. The radioles of *R. rosavendai* appear to be distinct from those of the Eocene species *C. cubensis* in the same ways.

A species having radioles with flattened tips was described by Philip (1963, p. 198, pl. 22, figs. 6-8) as *Stylocardaris*? *chapmani*. His specimens were collected in Prejanjukian beds (Oligocene) of southeastern Australia. Without tests of *C. cubensis*, comparisons between it and the Australian species are not possible, but certainly the radioles, at least distally, are very similar.

Tests and radioles of *Cidaris pratti* W. B. Clark are known from the middle and late Eocene of southern and southeastern United States. The *C. pratti* radioles are distinct from those of *C. cubensis*; they are spinulose, have shorter collars, and appear, from extant material in USNM collections, never to be flattened.

Material. — SUPTC 10241, four radiole fragments from Palmer locality 942, Cuba. The holotype, "Tipo 301" in the Sánchez Roig collection, was not available for study.

Stratigraphic occurrence and locality. — Highest upper Eocene (Consuelo Formation), Cuba.

Measurements. — Two flattened radiole fragments, one 6.4 mm wide $\times$ 1.1 mm thick, other at least 8 mm wide (end now broken) $\times$ 1.2 mm thick. Midshaft fragment 2.7 mm wide, with 11 serrate ridges 0.3-0.4 mm wide and spaced 0.6-1 mm apart, serrations projecting to about 0.55 mm. In proximal fragment of radiole, missing milled ring and base, shaft 2.8 $\times$ 2.6 mm at the widest; 16 serrate ridges mostly 0.2 mm wide and spaced 0.2-0.8 mm apart, serrations projecting no more than 0.3 mm; minute serrate ridges (remnants of hair coat?) 0.08 mm or a little more wide; collar 1.75-1.9 mm long, 2.7 mm wide distally, 2.8 mm proximally.

Genus **CALOCIDARIS** H. L. Clark

Calocardaris palmeri, new species

Plate 3

Diagnosis. — Test low; pores subconjugate; primary tubercles

with distinct, but shallow, crenulations along upper margin of platform on plates at and adapical to ambitus; areoles all separated by at least one row of scrobicular tubercles; ambital radioles slender and long (about equal to horizontal diameter of test); shaft shiny, with eight to 10 entirely smooth ridges, these microscopic on lower part of shaft; collar short.

Description.—Holotype and only known specimen includes large fragment of large test. Apical margin lacking but vertical diameter estimated to be little more than half horizontal diameter. Adoral margin neither flattened nor incurved. Width of peristome about 35 per cent horizontal diameter of test. Ambulacra slightly sinuate, slightly more than one-fourth width of interambulacra. At ambitus, 14 to 15 ambulacral plates per interambulacral plate. Pores oval, about equal in size, separated by wall at least as wide as a pore and low enough for pores to be considered subconjugate. Interporiferous area equal in width to one poriferous area, that of each plate with large marginal tubercle and one slightly smaller inner tubercle.

Seven or eight interambulacral plates per column. Areoles about 60 per cent width of plate, only slightly depressed, all separated by at least one row of scrobicular tubercles. Primary tubercles moderately high; on plates at ambitus and above, platform crenulate along adapical edge. Scrobicular tubercles round, not prominent, separated by small tubercles. Circle of slightly smaller tubercles outside scrobicular tubercles. Median area otherwise covered by smaller, widely spaced tubercles that decrease in size to the sutures and are separated by distinct grooves.

Many radioles adherent to test or closely associated with it in matrix. Ambital radioles slender, in length about equal to horizontal diameter of test; some slightly flattened; some slightly curved. Shaft shiny, either entirely smooth or with eight to 10 very low, smooth ridges, these microscopic proximally but more apparent near tip. Tip either slightly widened and prominently ridged or not widened and having oblique, slightly indented end. Collar short, about 1.2 times as wide as proximal limits of collar. Base about 1.3 times wider distally than proximally. Half of circumference of acetabulum crenulate on ambital and adapical radioles but no crenulations on radioles from plates below ambitus.

Transitional radioles shorter, slightly curved, prominently

ridged on distal third; tips ridged and slightly widened and flattened. Oral radioles slightly curved, with low lateral ridges either entirely smooth (on basicoronal plates) or very slightly serrate; tips of radioles nearest oral margin of test rounded, flattened and ridged. Scrobicular spines long, broad, slightly flattened, excavate on one surface. Other secondary spines long, slender, slightly flattened.

Discussion. — R. H. Palmer recognized the one known specimen of *Calocidaris palmeri* as an undescribed species and labelled it with a name that he apparently anticipated using in a publication on his collection of Cuban fossil echinoids. He assigned it to the genus *Porocidaris*, thus indicating affinities with Recent species of *Histocidaris*, most of which formerly were referred to *Porocidaris* Desor. With its large test, crenulations on the tubercles, and long, scarcely tapering radioles, the specimen does resemble histocidarids, particularly *Histocidaris magnifica* Mortensen, a Philippine species. However, it bears even greater resemblance to *Calocidaris micans* (Mortensen), a species now living in Caribbean seas.

C. palmeri differs from histocidarids in four ways: its tubercles are crenulate only on the upper margin and never so deeply as in histocidarids; all of its interambulacral plates are separated by at least one row of scrobicular tubercles (all but the uppermost two or three are confluent in histocidarids); its pores are subconjugate (nonconjugate in histocidarids); its oral radioles are not as strongly serrate or curved; and its ambital radioles are more slender (maximum width 3 mm or more in histocidarids; 3.5 mm in *H. magnifica*) and have completely smooth ridges (radioles in all histocidarids except *H. magnifica* bear serrations or spinules).

C. palmeri differs from *C. micans* in several respects. Only in the smallest specimen of *C. micans* examined (USNM 10705 of 28.5 mm HD) is the wall between the pores as wide as in *C. palmeri*; in all larger specimens of *C. micans*, the wall is very narrow and high (well illustrated in USNM 10717 (48 mm HD) by Phelan, 1970, pl. 2, figs. 1, 6). In *C. palmeri*, all but the basicoronal tubercles show distinct though shallow crenulations along the upper edge of the platform, but in *C. micans* of comparable horizontal diameter, crenulations are either very faint or absent; only in smaller (28 mm to 48 mm) *C. micans* are crenulations distinct and then they are limited to plates above the ambitus. In these two respects, then, the

young of the Recent species recall the adult condition in the fossil. The areoles of *C. palmeri* are all separated by at least one row of scrobicular tubercles whereas the lower two in *C. micans* are confluent. There are only eight to 10 ridges on shafts of *C. palmeri* radioles but as many as 16 in *C. micans*. The ambital radioles of *C. palmeri* are about equal in length to the horizontal diameter of the test but exceed the horizontal diameter considerably in *C. micans*. The test is lower in *C. palmeri* (56 per cent of HD) than in *C. micans* (61 to 85 per cent of HD).

C. micans has been reported from depths of 200 to 330 m. The Güines Formation, in which *C. palmeri* was found, apparently was deposited in not very deep water over the insular shelf.

In naming the species, I should have preferred to honor Palmer's intentions, but his chosen specific name seems better applied to a species with thorny radioles. Instead, this magnificent species is named for Dr. Palmer.

Holotype. — ANSP 50974, a large portion of one test and a number of associated radioles, secondary spines and teeth, all embedded in matrix, and some loose radioles; collected by R. H. Palmer at Palmer locality 978, Habana Province, Cuba.

Material. — In 1963, I examined the holotype and only known specimen, borrowing it from the Museum of Paleontology, University of California, Berkeley, which had it and other Palmer specimens on loan from the Academy of Natural Sciences, Philadelphia. In 1976, when I asked to reborrow the specimen from the ANSP, it could not be located. Expecting that it eventually will be found and believing it important to call attention to the presence in the Caribbean Miocene of a *Calocidaris*, I am including the new species description as originally planned. Photographs of the specimen have been sent to the ANSP to represent the holotype until it is relocated.

Stratigraphic occurrence and locality. — middle Miocene (Güines Formation, Basal Yumurí limestones), Cuba.

Measurements of holotype. — Test: estimated 60-65 mm in HD, 35 mm in VD (approx. 56% HD); PerD 22 mm (approx. 35% HD); ApSD unknown; IAmW at ambitus 25 mm; AmW 7 mm (28% IAmW); IAmPIW (ambital) 15 mm; ArW 9 mm (60% IAmPIW); MAW 4 mm (27% IAmPIW); AdrAW 2 mm; IPorAW 2.5 mm; PorAW 2.5 mm. Largest ambital radiole: length 65 mm; width 2.4 mm; collar 1.9 mm long, 2.4 mm wide distally, 3.5 mm

wide proximally; milled ring 4.2 mm wide; base 1.8 mm long, 3.8 mm wide distally, 2.9 mm wide proximally. Scrobicular spines to 7.2 mm long, 1-1.5 mm wide; other secondary spines 4.8-6 mm long, 0.3-0.5 mm wide.

Genus **TRETOCIDARIS** Mortensen

Tretocidaris anguillensis, new species

Plate 2, figures 9-12

1866. *Cidaris melitensis* Wright, Guppy, p. 299.
 1867. *Cidaris melitensis* Wright, Guppy, p. 44; 1921 reprint, p. 192.
 1869. *Cidaris melitensis* Wright, Etheridge in Sawkins, p. 335.
 1875. *Cidaris Melitensis* Wright, Cotteau, p. 8, pl. 1, figs. 1-10.
 1876. *Cidaris Melitensis* Wright, Cotteau, p. 126.
 1882. *Cidaris melitensis* Wright, Guppy, p. 194; 1921 reprint, p. 103.
 1887. *Eucidaris melitensis* Wright, Döderlein, p. 42.
 1922. *Cidaris melitensis* Wright, Jackson [part], p. 21, pl. 1, figs. 12-17.
 [Not specimens from Dominican Republic]
 1922. *Cidaris melitensis* Wright, Lambert, p. 594.
 1927. *Cidaris melitensis* Wright, Arnold and Clark, p. 11, pl. 1, figs. 12-17.
 1928b. *Cidaris melitensis* Wright, Mortensen [part], p. 341. [Not Maltese reports]
 1955. *Cidaris melitensis* Wright, Casanova, p. 2.
 [probably not *Cidaris melitensis* Wright, Sánchez Roig, 1949, p. 26; probably radioles of young *Phyllocanthus peloria* (Jackson)]

Diagnosis. — Test medium size (maximum known HD 25 mm), low. Apical system and peristome about equal in size. Ambulacra more than one-third width of interambulacra. Pores spaced more than one pore width apart and subconjugate. Two inner tubercles on interporiferous area of each plate in zigzag arrangement. Up to six or seven interambulacral plates per column. Median interambulacral sutures bare.

Description. — Two tests examined (16 mm and 25 mm in HD) low in profile, flattened adapically and adorally. Apical system and peristome about equal in diameter. Ambulacra nearly straight, 40 per cent or more width of interambulacra. Nine ambulacral plates adjoining interambulacral plates at ambitus in largest specimen, eight in other. Poriferous areas only slightly depressed. Pores separated by wall about two pore widths wide. Upper part of wall between pores high but groove on lower part of plate wide enough that pores are considered subconjugate. Interporiferous area 1.7 to 1.9 times as wide as one poriferous area. Marginal tubercles contiguous and in regular series; at ambitus, each plate usually having two, rarely one, slightly smaller, closely spaced tubercles in zigzag arrangement; inner tubercle nearest marginal situated low on plate,

other nearer middle. Some inner tubercles apparently mamelonate. Area adjacent to median suture bare.

Six to seven interambulacral plates per column in largest specimen, five to six in other. Areoles not depressed and about two-thirds width of plate; those on lower two plates confluent, others separated by row or two of scrobicular tubercles. Scrobicular tubercles prominent, separated by small tubercle or ridge. Ring of slightly smaller tubercles outside scrobiculars; remainder of plate bare to sutures. Median and horizontal sutures slightly depressed. Primary tubercles only moderately high, smooth on largest specimen but crenulate on upper edge of adapical tubercles in small specimen. In latter, upper edge of platform on best preserved plates "beaded" by crenulations.

Three radioles (USNM 115399 c-e), apparently collected with Anguillan tests, lacking all ornamentation except for few nodules near collar; remnants of anastomosed hairs, similar to those of fossil eucidarid radioles, between nodules.

Discussion. — *Cidaris melitensis* Wright (1855), to which Guppy and others referred the Anguillan specimens, is a Maltese species. Certainly the Anguillan tests resemble the type-specimens of *C. melitensis* in many respects, but their ambulacra are wider and generally have fewer ambulacral plates per interambulacral plate at the ambitus, more inner tubercles on the ambulacral plates (see Table 5), and pores that are subconjugate. In *C. melitensis*, at least in the types, there is only a very narrow groove between the wall of one plate and the ridge on the next plate below. Other specimens from Malta in the British Museum (Natural History), labelled *Cidaris melitensis*, have pores more like those in the Anguillan specimens but differ from the latter in all the other features mentioned above. Additional differences between the two species are more extensive bare areas in interambulacra and "beaded" edges on platforms of crenulate tubercles in *Tretocidaris anguillensis*. It is doubtful that the Anguillan and Maltese specimens are conspecific.

Mortensen (1928b, p. 335) suggested that *C. melitensis* is closely related to *Stylocidaris affinis* (Philippi), perhaps the ancestor of it. The Anguillan tests also resemble *S. affinis* to considerable extent, but with their bare areas, equal-sized apical system and peristome, "beaded" crenulations and more widely spaced pores,

they are nearer to *Tretocidaris bartletti* (A. Agassiz), now living in the Caribbean. *T. anguillensis* may well be the latter's ancestor. From both *S. affinis* and *T. bartletti*, the Anguillan tests differ with respect to number of ambulacral plates per interambulacral plate and wider ambulacra (Table 5).

Although *T. anguillensis* and *C. melitensis* are considered distinct here, similarities between the two indicate they may be linked phylogenetically. A suggested evolutionary trend, mentioned also in the discussions of species of *Cidaris* and *Calocidaris*, of reduced width of the wall between the pores (in effect narrowing the relative width of the ambulacrum) makes it seem unlikely (when Table 5 is considered) that the Caribbean species derived from the Maltese species. *T. bartletti* is confined to warm waters, which indicates there may also have been little temperature tolerance in *T. anguillensis*; if so, descent of *C. melitensis* from the Caribbean species would seem unlikely. The two fossil species may have had a common ancestor in Tethys.

Arnold and Clark (1927, p. 11) recorded a small specimen of *C. melitensis* from Jamaica. This specimen could not be located at the Museum of Comparative Zoology or elsewhere and was not figured by Arnold and Clark. The only measurements (HD 13 mm; VD 7 mm; ApSD = PerD 5.5 mm) are what would be expected of a small specimen of *T. anguillensis*.

Jackson (1922, p. 21) referred to *C. melitensis* a radiole fragment from USGS locality 8583 (Miocene, Trinidad) and two small radioles from USGS locality 8519 (Miocene, Dominican Republic). The first is referred here to *Prionocidaris cojimarensis* and the latter are referred to *Eucidaris madrugensis* (Sánchez Roig).

Holotype. — USNM 115399a, the largest (crushed) test collected by P. T. Cleve at Cleve locality (a) in the Anguilla Formation of Anguilla; apparently illustrated by Cotteau (1875, pl. 1, figs. 1-4), although those figures are freely restored.

Paratypes. — USNM 115399b, c-e, the smaller test and three radioles that were collected with the holotype.

Material. — The type-specimens cited above were examined. Three other test fragments (USNM 115412), collected by Cleve in the Anguilla Formation, could not be located. These specimens were part of the Guppy collection before being deposited in the [U.S.]

Table 5. — Selected test characters (last three as numbers) of *Stylocidaris affinis* (USNM 12948, both columns); *Cidaris melitensis* (type-specimens, Bristol Museum 6589, left column; BM E43295-E43299, right column); *Tretocidaris anguillensis* (USNM E11399 b and a, left and right columns, respectively); and *Tretocidaris bartletti* (USNM E11901, left column; USNM E11902-E11903, E11897, 6836, right column).

Characters	S. affinis		C. melitensis		T. anguillensis		T. bartletti	
Pores	nonconjugate		nonconjugate		subconjugate		nonconjugate or subconjugate	
HD (mm)	10-20	23-30	21.5-26.5	17.5-25	16	24	15	23-28
ApSD/HD (%)	51-59	49-54	44-48	†	50	50	47	35-50
PerD/HD (%)	44-50	43-52	45-55	†	50	50	47	41-45
AmW/IAmW (%)	27	28	28-32	24-36	40	42	29	23-28
AmPl:IAmPl	9	10-13	11	10-12	8	9	11	11-14
IAmPl:Col	4-6	5-7	5-6	5-7	5-6	6-7	5	6-7
IPorTub	M+1	M+1-2	M+1-2*	M+0-1	M+1*-2	M+1*-2	M+0	M+0-1

* = rarely, † = not measured, but approximately equal.

National Museum of Natural History. As mentioned above, the Arnold and Clark specimen from Jamaica also could not be located.

Stratigraphic occurrence and locality. — upper lower Miocene (Anguilla Formation), Anguilla.

Measurements. — Tests, holotype and paratype, respectively: HD 24 and 16 mm; VD 14 and 8 mm (58 and 50% of HD); PerD 12 and 8 mm; ApSD 12 and 8 mm; IAmW 9.5 and 7 mm; AmW 4 and 2.8 mm (42 and 40% of IAmW); IAmPIW 5.5 and 4 mm; ArW 3.4 and 2.7 mm (64 and 67% of IAmPIW); MAW 1.3 and 0.9 mm (25% of IAmPIW in both specimens); AdrAW 1.7 and 1.4 mm; PorAW 0.9 and 0.8 mm; IPorAW 1.7 and 1.4 mm; IAmPl:Col six to seven and five to six; AmPl:IAmPl at ambitus nine and eight; IPorTub:AmPl M+2 or (rarely) M+1 in both specimens.

Radioles: 21, 20, 12 mm long; largest specimen 2.5 mm at widest; nodules remaining at proximal end of shaft in 14 to 15 series 0.25-0.3 mm wide; collar 0.5-0.6 mm long on all three, 2.1-2.2 mm wide distally on two, 1.6 mm wide on smallest, not widened proximally; milled ring worn on all but probably was only slightly wider than proximal end of collar; base 0.7-1 mm long on the three specimens, 2.1 mm wide distally on the largest two, 1.6 mm on other, 0.3-0.5 mm narrower proximally.

Genus **PALMERIUS**, new genus

Type-species. — *Palmerius roberti*, n. sp., described from specimens collected by R. H. Palmer at Palmer localities 1102 and 1640 (Eocene of Cuba).

Diagnosis. — Same as for species.

Discussion. — The radioles of the type-species recall those of Recent *Stylocidaris? fusispina* Mortensen (1928a, p. 72) but differ in being cylindrical as well as fusiform (only fusiform in *S.? fusispina*) and having considerably longer collars. Mortensen (1928b, p. 334) remarked that *S.? fusispina*, because of the characters of its radioles, stands apart from other stylocidarid species, and he doubted it belongs in that genus. He indicated that *S.? fusispina* shows affinities with species of *Acanthocidaris* but could not be considered congeneric with them because of the much longer collars, differently shaped radioles and much more strongly crenulate tubercles in the latter.

Because the radioles of *Palmerius roberti* and *S.?* *fusispina* are similar and differ in the same ways from radioles of stylocidarids and acanthocidarids, there is reason to believe the tests may also be similar enough for the Recent species to be referred to *Palmerius*. Determination of this, however, awaits discovery of tests associated with *P. roberti* radioles.

The genus-name is masculine. The name honors Dr. Robert H. Palmer whose collection of fossil cidaroids is the basis for a large part of this paper.

Stratigraphic occurrence and locality. — Eocene of Cuba.

Palmerius roberti, new species

Plate 4, figures 1-4

Diagnosis. — Test unknown. Radioles fusiform or cylindrical; shaft with ridges that are entirely smooth except near collar where they may give way to series of nodules; surface between ridges in most of known specimens covered with closely set, small granules that may be remnants of dense hair coat; collar up to 2 mm long; milled ring inconspicuous; acetabulum perforate, distinctly crenulate along one edge and sometimes faintly crenulate on other.

Description. — Radioles long, slender, slightly tapered or short, wide, fusiform. Tips not preserved on material examined. Shaft with 12 to 16 ridges, these crenate near collar in some specimens but otherwise smooth. In most specimens, surface between and up sides of ridges densely covered with small granules, possibly remnants of hairs. In one small, apparently young, specimen, surface of grooves glistening and smooth except for slight irregularities reflecting underlying septal ridges and "waves" of apparently incipient granules. In some specimens, shaft smooth for short distance (0.2 to 1.4 mm) above collar. Collar moderately long (up to 2 mm), slightly widened toward milled ring; on some specimens, septal ridges of collar more or less granular. Milled ring scarcely wider than proximal end of collar. Base shorter than collar, with distal diameter 1.05 to 1.5 times proximal. Acetabulum, where intact, distinctly crenulate along one edge, sometimes faintly crenulate on opposite edge, perforate.

Discussion. — The radioles of *Palmerius roberti* are distinct from all others known from the Caribbean. They are most like those of *Stylocidaris?* *fusispina* Mortensen, presently living in Japanese seas, but differ in having longer collars, cylindrical as well as fusiform

shapes, a larger maximum number of ridges (10 to 12 are reported for *S. fusispina*), and only closely spaced nodules between the ridges rather than a dense hair coat. The latter two differences are not necessarily significant in distinguishing the two species; hairs rarely remain intact on fossil radioles so the minute nodules likely are remnants of a dense hair coat, and the difference in numbers of ridges may be due to the *S. fusispina* specimens' being small and, according to Mortensen, appearing not yet adult while the fossil radioles appear "finished," i.e., from adult specimens.

The radioles of *P. roberti* resemble somewhat a few of the smooth-ridged radioles figured by Philip (1964, pl. 65, figs. 1, 4-16) as *Goniocidaris? pentaspinosa* Chapman and Cudmore, from the Oligocene and Miocene of Australia. However, they obviously are not the same, because many of the Australian radioles are spinulose and have neither cortical hairs nor, apparently, crenulate acetabula.

There is also some resemblance to radioles of some European Eocene species, e.g., *Cidaris acicularis* d'Archiac (illustrated by Cotteau in d'Orbigny, 1889-1894, pl. 306, figs. 5-6) and *Cidaris subprionata* Rouault (see Cotteau in d'Orbigny, 1889-1894, pl. 306, fig. 20), but the ridges in these appear to be different and the acetabulum is either smooth (in *C. acicularis*) or deeply crenulate around the entire circumference (in *C. subprionata* and some *C. acicularis*).

Holotype.—SUPTC 10242a, a fusiform radiole collected by R. H. Palmer at Palmer locality 1640, Camagüey Province, Cuba.

Paratypes.—PRI 29632, 29760; LSJU 53244; SUPTC 10242b-h; 10243.

Material.—

Locality	Catalogue Number	Collector	Number of radiole specimens
Bermúdez 337	PRI 29760	P. J. Bermúdez	2
Palmer 52	LSJU 53244	R. H. Palmer	3
Palmer 1102	PRI 29632	R. H. Palmer	34
Palmer 1102	SUPTC 10243	R. H. Palmer	6
Palmer 1640	SUPTC 10242a (holotype)	R. H. Palmer	1
Palmer 1640	SUPTC 10242b-h	R. H. Palmer	7

Stratigraphic occurrence and locality.—lowest upper Eocene (Jabaco Formation), Cuba.

Measurements.—Holotype: 22 mm long, minus tip, 4.5 mm at widest, 2.7 mm wide where broken distally. Shaft with 17 ridges 0.15-0.2 mm wide and spaced 0.4-1 mm apart. Neck 1.5 mm long;

collar 1.5 mm long, 2.7 mm wide distally, 2.8 mm proximally; milled ring 2.9 mm wide; base 1.2 mm long, 2.6 mm wide distally, 1.9 mm proximally.

Paratypes: long, slender radioles estimated to reach 50 mm or more in length, stout, fusiform radioles probably not more than 35 mm long; width 1.7-2.9 mm in the slender type, 3-4 mm in the fusiform specimens. Shaft with 12 to 16 ridges 0.19-0.4 mm wide and spaced 0.2-1 mm apart; minute nodules (remnants of hairs?) usually 0.08 mm in diameter but ranging from slightly smaller to almost 0.2 mm. Collar usually 1.2-1.5 mm long but ranging from 1-2 mm, very slightly narrower than the shaft distally and 0.05-0.6 mm wider proximally. Milled ring 0.05-2 mm wider than proximal end of collar. Base 0.7-1.4 mm long and 1.05-1.5 times wider distally than proximally.

Genus **EUCIDARIS** Döderlein

Eucidaris tribuloides (Lamarck)

1816. *Cidarites tribuloides* Lamarck, p. 56.
 1887. *Eucidaris tribuloides* (Lamarck), Döderlein, p. 42, 51, pl. 9, fig. 2.
 1908. *Cidaris minor* Koehler, p. 302, pl. 15, figs. 136-138.
 1909. *Eucidaris tribuloides* var. *africana* Mortensen, p. 40.
 1955. *Eucidaris tribuloides africana* forma *attenuata* A. M. Clark, p. 51, pl. 2.
 1968. ?*Cidaris tribuloides* (Lamarck), Maloney and Macsotay, p. 276, 281.
 1969. *Eucidaris tribuloides* (Lamarck), Weisbord, p. 287, pl. 14, figs. 7-9, pl. 15, figs. 4-5 [includes complete synonymy of species and illustrations of radioles from the Pliocene and Pleistocene of Venezuela].
 [Not *Cidaris tribuloides* (Lamarck), Jackson, 1922, p. 23, pl. 1, figs. 18-20; Sánchez Roig, 1926, p. 32; Sánchez Roig, 1949, p. 25; = *Eucidaris madrugensis* (Sánchez Roig)]

Description. — Test medium-sized (HD 60 mm or less), low in profile, commonly somewhat flattened adapically and adorally, in some specimens incurved at peristomial edge. Peristome width about 30 (in large specimens) to 60 (in young specimens) per cent horizontal diameter of test and nearly equal to apical system width in specimens 17.5 mm or more in diameter, although in small specimens apical system usually slightly larger (see Appendix). Ambulacra slightly sinuate, one-fifth to one-third width of interambulacra. At ambitus in large specimens, nine to 10 ambulacral plates per interambulacral plate. Interporiferous area 1.2 to 5 times (average 2.6 in 28 specimens) as wide as one poriferous area. Poriferous areas slightly depressed. Pores slightly oblique, separated by wall no wider than one pore width and raised into distinct knob. Ridge along

upper part of plate depressed in center in older specimens. Interporiferous area of each plate having marginal tubercle and commonly one or two smaller, crowded, inner tubercles.

Up to 10 interambulacral plates per column. Areoles about two-thirds to three-quarters plate width in small specimens, nearer one-half plate width in large specimens; confluent on two to four basiconal plates but otherwise separated by one or two rows of scrobicular tubercles. Primary tubercles moderately high in comparison to those in other cidaroid species; platforms usually smooth although crenulate along upper margin on adapical plates in some young specimens. Scrobicular tubercles nearly circular, separated by small tubercle or ridge. Remainder of plate to sutures covered with smaller, more or less equal-sized, closely spaced tubercles, these horizontally aligned in large specimens, particularly on plates above ambitus, but not separated by distinct grooves. Median suture only slightly depressed in specimens examined but "sometimes distinctly sunken" (Mortensen, 1928b, p. 402).

Radioles variable. Typically, length about equal to or less than horizontal diameter of test; maximum width 3 to 4.5 mm; shaft with gradual taper to obtuse tip. In other specimens, radioles with clavate shape or long, tapered to acute tips; some long radioles bulging to 5 mm on proximal portion of shaft. Fluted radiole tip with central prominence, often cited as eucidarid character, most typical in young individuals or in newly regenerated radioles but commonly worn or otherwise modified in older specimens. Shaft having 14 to 27, usually 16 to 20, more or less regular longitudinal series of low nodules. Diameter of nodules 0.3 to 0.5 mm on typical (30 to 40 mm long) radioles, 0.55 to 0.8 mm on some clavate specimens from Puerto Rico; smallest and most closely spaced on adoral surface of radiole, producing effect of slight flattening of that surface. Surface of shaft between and over nodules covered with dense but large-meshed mat of coarse, branching, anastomosing hairs. Neck very short, less than 0.5 mm long. Collars 0.4 to 2 mm long, only slightly, if at all, widened proximally. Milled rings not prominent. Bases commonly about 1.25 to 1.45 times wider distally than proximally. Acetabular edge usually smooth but adapical radioles of very young specimens may show faint crenulations on upper margin. Oral radioles smaller and usually slightly flattened. Scrobicular spines broad with blunt, concave tips.

Discussion.—In very young individuals, the radioles have sharply peaked nodules or low spinules. These persist longest in the transverse white bands, being replaced in the dark bands by lower, rounded nodules. These small radioles are distinctly verticillate. By the time the radioles are a little more than 10 mm long, the white banding has disappeared, and the radioles are more or less uniformly dark and nodulose, hence non-verticillate.

Mortensen (1928b, p. 405) called attention to galls on radioles of over half of 15 specimens (USNM 10734) collected at "Albatross" station 2407 and attributed them to parasitism by a species of the gastropod *Stylifer*. Distortion of *Eucidaris tribuloides* radioles resembling gall formation can also be produced by sudden increase or decrease in growth rate brought about by environmental changes (Cutress, 1965, p. 819).

Mortensen, with only a few specimens, distinguished eucidarids from the Cape Verde Islands and Gulf of Guinea as *Eucidaris tribuloides* "var." *africana* on the basis of their having primary areoles wider than the interambulacral median area and having narrower valves of globiferous pedicellariae than in "typical" *E. tribuloides*. Pawson (1978, fig. 4), with larger samples, found that the relationships between areole and median area widths are not significantly different in West Indian and West African specimens. He also found that the relationship between the diameters of the peristome and apical system is similar in eucidarids from the two areas. In both median area width/areole width and apical system diameter/peristome diameter ratios, Pawson found eucidarids from St. Helena (*Eucidaris clavata* Mortensen) and Ascension Island to be distinct from the West African-West Indian species and concluded that the form from Ascension was conspecific with *E. clavata*. It should be noted that Mortensen and Pawson used the term "median area" in the usual sense, i.e., the entire area between areoles in adjacent columns in an interambulacrum, not as here (median area of a single plate).

As far as Mortensen's data for *E. clavata* are concerned, West Indian specimens of *E. tribuloides* examined during my study differ from *E. clavata* in additional respects: more interambulacral plates per column, fewer confluent primary areoles (all but two to four

adapical areoles per column are confluent in *E. clavata*), and no fan-shaped septal bundles in the radioles such as were found in *E. clavata*.

Jackson (1922, p. 23) and Sánchez Roig (1949, p. 25) referred to *E. tribuloides* several tests from the Miocene of Cuba. These, and eucidarid radioles from the Miocene of Cuba, have been assigned here to *Eucidaris madrugensis* (Sánchez Roig), discussed on succeeding pages where the distinctions between the two species are detailed.

Maloney and Macsotay (1968, p. 276) listed *Cidaris tribuloides* from the Cerro Gato Formation and Tortuga Formation, Punta Piedras Member, Venezuela, both Pleistocene in age. There are records also of fossil *Eucidaris tribuloides* radioles from the eastern Atlantic and Mediterranean areas, e.g., from Miocene deposits of the Azores (Mayer-Eymar, 1864, p. 12; Veiga Ferreira, 1961, p. 532, pl. 1, fig. 5; pl. 2, fig. 11) and in the Grand Canaries (Lyell, 1854 and Rothpletz and Simonelli, 1890, *vide* Darteville, 1953, p. 11), from the Pliocene of the Rhone Basin (Lambert, 1910, p. 9, pl. 1, figs. 41-43; Cotteau *in* d'Orbigny, 1889-1894, p. 736, pl. 11, figs. 11-14) and from the Pliocene of Sidi Cherif, Oran, Algeria (Lambert, 1931b, p. 84). Mortensen (1928b, p. 407) doubted the correctness of the Lambert and Cotteau identifications. Darteville (1953, p. 8, pl. 1, figs. 103; pl. A, figs. 3-4) recorded as *Eucidaris tribuloides africana* radioles from the Pleistocene of Angola which may very likely belong to *E. tribuloides*. According to Lambert (1910, p. 10), radioles of *Cidaris tessurata* Meneghini are identical with, and those of *Cidaris zeamis* Sismonda have certain resemblance to, radioles of *E. tribuloides*; both fossil species are from the Rhone Basin. Toula (1909, p. 735) found in an early Tertiary fauna of Gatún, Panama, two joined interambulacral plates 12 mm wide and 6.5 mm high that he thought resembled those of *E. tribuloides*. I saw none of these specimens, and from figures and descriptions alone it is uncertain which, if any, really are eucidarid.

Material. — Examined fossil radioles from Venezuela are listed below. Numerous Recent specimens in collections of the USNM, MCZ and Department of Marine Sciences, University of Puerto Rico at Mayagüez also were studied.

Locality	Catalogue Number	Collector	Number of radiole specimens
Weisbord D608	Weisbord collection	N. E. Weisbord	15
Weisbord D608a	PRI 27657	N. E. Weisbord	1
Weisbord K599a	PRI 27658	N. E. Weisbord	1
Weisbord S609a	Weisbord collection	N. E. Weisbord	1

Stratigraphic occurrence and localities. — Recent in the western Atlantic from North Carolina, Bermuda and the West Indies south to Brazil; Gulf of Mexico; eastern Atlantic from the Azores to the Gulf of Guinea. Playa Grande and Abisinia formations, Venezuela, considered Pliocene and Pleistocene, respectively, by Weisbord (1969) but both as Pleistocene by Dr. Oliver Macsotay (pers. comm., 1976). Cerro Gato and Tortuga Formations of Venezuela, both Pleistocene. Pliocene of Jamaica (Discovery Bay), according to the late Dr. Thomas Goreau (pers. comm., 1969).

Measurements. — For measurements of selected test characters of a series of Recent specimens, see the Appendix. Radioles: length equal to or less than HD of test, *i.e.*, not exceeding about 60 mm and usually less; shaft width about 4.5 mm at maximum but more commonly 3-4 mm; nodules in 14 to 27, but usually 16 to 20, series; width of nodules 0.2-0.8 mm but commonly 0.3-0.5 mm; collar length ranging from 0.4-2 mm but commonly 0.7-1.5 mm, one side commonly slightly longer than other; collar width about same throughout; milled ring 0.5-3 mm wider than proximal end of collar; base length ranging from 0.3-1.5 mm but usually 1-1.5 mm; base width 1.24-1.45 times greater distally than proximally.

***Eucidaris madrugensis* (Sánchez Roig)**

Plate 4, figures 5-10

1855. ?*Cidaris metularia* Lamarck, Michelin *in* Duchassaing, p. 758.
 1909. ?*Cidaris* spec., Toulou, p. 735.
 1922. *Cidaris tribuloides* (Lamarck), Jackson, p. 23, pl. 1, figs. 18-20.
 1926. *Cidaris tribuloides* (Lamarck), Sánchez Roig, p. 32.
 1937. ?*Cidaris thouarsii* Valenciennes, Jackson, p. 229.
 1949. *Cidaris tribuloides* (Lamarck), Sánchez Roig [part], p. 25 [probably only the USNM specimen].
 1949. *Dorocidaris madrugensis* Sánchez Roig [part], p. 29, pl. 1, fig. 4 [named *Leiocidaris madrugensis* in plate legend]. [not *Leiocidaris madrugensis* Sánchez Roig, 1949, pl. 1, fig. 2 nor *Dorocidaris madrugensis* Sánchez Roig, 1949, p. 32]
 1949. *Leiocidaris madrugensis* Sánchez Roig, pl. 1, fig. 4. [not *Leiocidaris madrugensis* Sánchez Roig, 1949, pl. 1, fig. 2]

Description. — Known tests up to 29 mm in horizontal diameter, low in profile, flattened adapically and adorally, some specimens in-

curved at peristomial edge. Apical system about same size or slightly larger than peristome. Ambulacra slightly sinuate, about one-fourth as wide as interambulacra. Eight to 10 (usually nine to 10) ambulacral plates per interambulacral plate at ambitus. Poriferous area slightly depressed. Pores slightly oblique, separated by wall equal in width to one pore and having distinct knob. Interporiferous area at ambitus one and one-half to two times width of one poriferous area. Marginal tubercles large, in regular series. Remainder of interporiferous area of each plate bare or with one inner tubercle slightly smaller than marginal tubercle forming zigzag series with those on adjoining plates; rarely a second, very small, inner tubercle.

Six to seven interambulacral plates per column. Areoles large, about two-thirds plate width at ambitus, those on lowermost two or three plates confluent. Tubercles moderately high; platforms smooth or with faint indications of crenulations along adapical margin. Scrobicular tubercles nearly circular, separated by small tubercles or ridge. Smaller tubercles of about equal size crowded on rest of plate to sutures.

Known radioles short, largest not longer than horizontal diameter of known tests, fusiform or more or less cylindrical, straight. Tip obtuse, fluted, with central prominence in best preserved specimens. Shaft with 16 to 20 longitudinal series of nodules. Some radioles, including largest, with two or more whorls of larger nodules, giving shaft a distinctly verticillate appearance; each whorl, with few exceptions, consisting of two or more transverse rows of nodules, these not continuous onto oral surface of radiole. Nodules otherwise smaller and more closely spaced on oral surface of radiole, giving this surface a very slightly flattened appearance. Surface of shaft on some specimens with remnants of dense coat of anastomosed hairs. Neck extremely short or altogether lacking. Collar short, scarcely widened proximally. Acetabulum smooth or with faint crenulations along one side.

One apparently oral radiole smaller, with less prominent nodules.

Discussion. — The foregoing description of radioles was drawn from a large number of specimens, in Palmer and Bermúdez collections, that are conspecific with the two radioles illustrated by Sánchez Roig (1949, pl. 1, fig. 4). Sánchez Roig indicated that his

radiole specimens were of Late Cretaceous age, but this apparently was a *lapsus*; all the specimens collected by Palmer and Bermúdez came from Miocene (? to Pliocene) strata.

Sánchez Roig (1949) created considerable confusion in naming the species. He used both *Dorocidaris madrugensis* (in the text) and *Leiocidaris madrugensis* (in the plate legend), not only for the two eucidarid radioles but also for a radiole fragment and an interambulacral plate that are not eucidarid at all but apparently referable to a Late Cretaceous phyllacanthid species, *Leiocidaris leoni* Lambert and Sánchez Roig in Sánchez Roig (1926) (here assigned to a new genus). One description of *D. madrugensis* (p. 32) and one illustration of *L. madrugensis* (pl. 1, fig. 2) refer clearly enough to the phyllacanthid specimens. However, in the other description of *D. madrugensis* (p. 29), he referred to both fig. 2 and fig. 4, and several aspects of that brief description could be interpreted as referring better to the radiole in fig. 2 (*L. leoni*) than to the two eucidarid radioles shown in fig. 4: "largas" (Sánchez Roig did not give magnifications for any of the figures in his paper, but the eucidarid radioles collected by Palmer and Bermúdez are not large, having a maximum length of 29 mm and commonly less; radioles collected by Palmer and the USGS and apparently conspecific with those of *L. leoni* are truly large); "con foceta articular áspera" (apparently indicating crenulate acetabula; in eucidarids, only in very small individuals are there slight crenulations on tubercles and acetabula, and the specimens illustrated by Sánchez Roig (fig. 4) definitely do not have an immature appearance; large tests from Jamaica and Cuba that appear to be conspecific with the *L. leoni* test fragments may have either distinctly crenulate or smooth tubercles); "collar bien pronunciado" (the collars of the two eucidarid radioles described by Sánchez Roig do not show in the illustration but collars of the radioles collected by Palmer and Bermúdez are not prominent, being not more than 1 mm long and commonly only 0.5 mm; collars in radioles that are apparently conspecific with the *L. leoni* fragments are usually 2 to 3.5 mm long). Further, the locality given with the description of *D. madrugensis* on p. 29 of the Sánchez Roig paper (Central San Antonio, Madruga, Habana) is the same as the Upper Cretaceous Palmer locality 757 from which Palmer collected a radiole fragment referable to *L. leoni*. Also, Sánchez Roig indicated there were radioles in his sample other than the two eucidarid speci-

mens. In sum, it seems very possible that Sánchez Roig inadvertently mixed two eucidarid radioles into a Cretaceous sample, in which case the eucidarid specimens might be considered still nameless. However, he is here given the benefit of some doubt in the matter, and the name *Leiocidaris madrugensis* is accepted as applying to both the eucidarid radioles in Sánchez Roig's fig. 4 and the two specimens in his fig. 2, although in the latter case the name goes into synonymy with *L. leoni*.

The description and measurements of *Cidaris tribuloides* given by Sánchez Roig (1949, p. 25) are from one of the tests (USNM 328221) here referred to *E. madrugensis*. Another specimen listed there under *C. tribuloides* (a test from Finca Santa Maria, Barrio Majagua, Ciego de Avila, Camagüey, an Eocene locality) is not eucidarid.

Eucidaris madrugensis can not be considered conspecific with *Eucidaris tribuloides*, a Recent, Pleistocene and possibly Pliocene, Caribbean species. The only whorled radioles found in *E. tribuloides* are on very young individuals, are no longer than 10 mm, and have only the beginnings of a hair coat. In *E. madrugensis*, whorls are common on radioles that, because of their size (up to 29 mm long) and the dense hair coat still evident on some, are apparently from adult specimens. Collars in *E. madrugensis* radioles are only about half as long as in radioles of comparable size of the Recent species. There are too few fossil eucidarid test specimens for close comparison, but in those that are known, the areoles are distinctly larger than in specimens of comparable size of the Recent species. (Compare Table 6 with measurements of *E. tribuloides* in the Appendix.) There are six to seven interambulacral plates per column in the fossil tests, six to eight in specimens of comparable size of the Recent species. There are eight to nine ambulacral plates per interambulacral plate in two of four known fossil test specimens, nine or ten in the other two; there are eight in all measured Recent specimens of comparable size.

E. madrugensis may have been the ancestor of *E. tribuloides*. If it was, the whorls of large nodules on the radioles must have disappeared in adults by the Pleistocene, and the two species may have been sympatric for a time in the Pliocene.

Although the Canimar Formation is late Miocene and Pliocene

in age, *E. madrugensis* apparently was present in the Caribbean earlier in the Miocene. Whorled eucidarid radioles that are indistinguishable from those of the Canímar have been collected at Cuban localities that have been placed in the lower to middle (or possibly upper) Miocene Cojímar Formation (Bermúdez loc. 83) and the middle Miocene Güines Formation (Palmer loc. 926).

Westward dispersals from early stocks of *E. madrugensis* may have carried that species into the eastern Pacific before closure of the Panamanian isthmus. There it could have speciated to *Eucidaris thouarsii* (Valenciennes) and *E. thouarsii galapagensis* Döderlein. Specimens from several eastern Pacific sites have been referred to *Eucidaris*: an interambulacral plate from the middle or upper Miocene of Panama (Toula, 1909, p. 735), a test fragment from the Miocene (Túxpan Formation) of Vera Cruz, Mexico (Jackson, 1937, p. 229), and the cast of a radiole from the Miocene or Pliocene of California (Arnold, 1908, p. 351; Loel and Corey, 1932, p. 167; Grant and Hertlein, 1938, p. 8; Hertlein and Grant, 1960, p. 104). In the UCMP collections, there are radioles labelled *Eucidaris* sp. aff. *thouarsii* from the Miocene of Baja California. Only the latter specimens (nine fragments from UC loc. B-3033) were seen during this work. Several of these are distinctly flattened and wider and have more series of nodules (28 to 30) than are usual in *Eucidaris* radioles, but the others do appear to be eucidarid. They differ from *E. madrugensis* in having longer collars (1 to 1.5 mm) and in lacking any signs of whorls in the nodules of the shaft.

With respect to the widths of the primary areoles in relation to interambulacral plate width and the number of ambulacral plates per interambulacral plate, *E. madrugensis* resembles *E. thouarsii* more than *E. tribuloides* (compare values in Table 6 with those for specimens 20 to 30 mm in horizontal diameter of the two Recent species in the Appendix), but in most other features it is more like *E. tribuloides*.

In Table 6 and elsewhere in this paper, measurements of median area widths were taken from individual plates, not the entire area between primary areoles (as in studies of Recent species). My usage is based on the fact that many cidaroid fossil test specimens are isolated interambulacral plates or only one-half of an interambulacrum. Chesher (1972, fig. 2) and Pawson (1978, fig. 4) considered median

area width/areole width ratios especially important in distinguishing *E. tribuloides*, *E. thouarsii* and *Eucidaris clavata* Mortensen, the latter living only on Ascension and St. Helena islands. For comparison with their figures (involving entire median areas), measurements are given here for the entire median area in the four specimens of *E. madrugensis* cited in Table 6: 3 mm in the 29 mm, 27.5 mm and 26 mm specimens, 2.5 mm in the smallest, giving median area width/areole width ratios of 0.55, 0.6, 0.75, 0.6 (mean 0.6). This mean appears to be near but slightly lower than that for 20 to 30 mm *E. tribuloides* (ratios approx. 0.6-0.8) plotted by Chesher (Pawson's specimens were larger). The ratios for *E. madrugensis* are distinctly higher than those (approx. 0.25-0.4) plotted by Chesher for 20 to 30 mm *E. thouarsii*. However, in six *E. thouarsii* within this size range which I measured, entire median area width/areole width ratios were 0.4 to 0.78 (mean 0.57), corresponding very nearly with those for *E. madrugensis*. I did not measure entire median areas in *E. tribuloides*.

In areole width per interambulacral plate width (Table 6 and Appendix), the similarity between *E. madrugensis* and *E. thouarsii* and the difference between those two and *E. tribuloides* is more marked; for 20 to 30 mm specimens: 54 to 64 per cent (mean 58) in *E. tribuloides*, 64 to 73 per cent (mean 68) in *E. thouarsii*, and 65 to 71 per cent (mean 67) in *E. madrugensis*.

In these 20 to 30 mm specimens, median area width per interambulacral plate width does not vary appreciably in the three species, but when more complete size ranges of the two Recent species are considered (see Appendix), median areas are distinctly wider and areoles smaller in *E. tribuloides* than in *E. thouarsii*.

Pawson (1978, fig. 5) found the ratio of apical system diameter to peristome diameter to be distinctly different in *E. tribuloides* and *Eucidaris clavata* Mortensen. Measurements made during my study indicate there is a similar difference between *E. tribuloides* and *E. thouarsii*. In *E. tribuloides*, apical system diameter/peristome diameter ratios were 1.0 to 1.3 (mean 1.05) in 16 specimens 5.75 to 14 mm in horizontal diameter; in 26 specimens from 17 to 50 mm in horizontal diameter, this ratio was 0.78 to 0.95 (mean 0.81) in 12 and 1.0 to 1.3 (mean 1.1) in the other 14. In 23 specimens of *E. thouarsii*, on the other hand, only two (HD 8.25 and 11 mm) had

ratios of 1.0; in all others but one, ratios were 0.7 to 0.9 (mean 0.84), *i.e.*, the peristome was larger than the apical system. *E. madrugensis* may be nearer *E. tribuloides* in this respect; in three specimens for which diameters of apical system and peristome could at least be estimated, ratios were 0.9, 1.0, 1.3, respectively, for the specimens 26 mm, 27.5 mm and 29 mm in horizontal diameter.

Eucidaris was represented in New Zealand as early as the late Eocene and on into the middle Oligocene by *E. strobilata* Fell (1954, p. 47, pls. 8A, E-H, J, 10B, 11E). A similar form from the lower Miocene of southeastern Australia was designated as *E. strobilata felli* by Philip (1963, p. 202, pl. 22, figs. 1-2, 5, 9). Included in the New Zealand material are several forms of radioles besides those that are typically eucidarid. One of these forms (Fell's pl. 8A), having protuberances on straight ridges that are separated by prominent grooves, is of particular interest, because ridged radioles that appear noneucidarid in form were collected from four of the Caribbean localities from which typical eucidarid radioles were collected and occurred at no localities where eucidarid specimens were not present. Tips of all these Caribbean specimens are missing, so it is not possible to determine if they had a eucidarid-type prominence such as the ridged specimens from New Zealand apparently have. They show no evidence of having had a hair coat and are longer (up to 32 mm without tips) than the New Zealand specimens (to 23 mm). Despite the coincidence in collection sites, the striking difference between the Caribbean ridged radioles and radioles of Recent eucidarids and the lack in Recent eucidarid species of such a completely different form of radiole has precluded for the present referral of the Caribbean ridged specimens to *E. madrugensis*. They are placed here in indeterminate genus A.

On the other hand, two other Caribbean fossil cidaroid radioles (USNM 242729, from the Gurabo Formation, upper Miocene to Pliocene, Dominican Republic), despite their distinct ridges, are referred questionably here to *E. madrugensis*, largely on the basis of their tips, which are obtuse, ridged and have a central prominence, *i.e.*, are typically eucidarid. They are quite unlike the ridged radioles of indeterminate genus A. They have some similarity to ridged radioles assigned here to *Prionocidaris cojimarensis*, but the few intact tips of the prionocidarid specimens do not resemble those of *Eucidaris*.

Material. — Sánchez Roig's specimens, "Tipo No. 101 Colección Sánchez Roig," were not seen.

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez 5	ANSP 50976	P. J. Bermúdez	—	8
Bermúdez 5	PRI 29608	P. J. Bermúdez	—	9
Bermúdez 39C	PRI 29609	P. J. Bermúdez	—	14
Bermúdez 54	PRI 29610	P. J. Bermúdez	—	35
Bermúdez 83	PRI 29611	P. J. Bermúdez	—	18
Bermúdez 299	PRI 29612	P. J. Bermúdez	—	48
Bermúdez 302	PRI 29613	P. J. Bermúdez	—	7
Palmer 377	PRI 29614	R. H. Palmer	—	4
Palmer 378	PRI 29615	R. H. Palmer	—	3
Palmer 898P	ANSP 50975	R. H. Palmer	1	—
Palmer 898P	PRI 29616	R. H. Palmer	—	36
Palmer 926	PRI 29617	R. H. Palmer	—	9
Palmer 932	PRI 29618	R. H. Palmer	—	5
Palmer 1189	PRI 29619	R. H. Palmer	—	18
Palmer 1393	PRI 29620	R. H. Palmer	—	4
Palmer 1554	PRI 29621	R. H. Palmer	—	15
Palmer 1593	PRI 29622	R. H. Palmer	—	8
USGS 5255	USNM 328221a-g	F. P. Black	7	—
USGS 8159	?USNM 242729	T. W. Vaughan <i>et al.</i>	—	2

? = questionably referred to species

Stratigraphic occurrence and localities. — middle Miocene (Güines Formation, upper and lower Yumurí Gorge series); lower to middle (possibly upper) Miocene (Cojímar Formation) and upper Miocene to Pliocene (Canímar Formation), Cuba. Possibly also upper Miocene to Pliocene (Gurabo Formation), Dominican Republic. According to Sánchez Roig (1949), his *E. madrugensis* specimens were found in Upper Cretaceous deposits; as mentioned above, this probably is a *lapsus*.

Jackson (1922) questioned the Miocene age of USGS 5255 because tests (USNM 328221) collected there "occurred in the same lot with *Echinometra prisca* and *Echinoneus cyclostomus*, both of which are found in the Oligocene of Anguilla." Presumably, the latter specimens came from the Anguilla Formation, now considered Burdigalian in age (Eames *et al.*, 1962).

Measurements. — See Table 6 for test measurements. Large radioles: 29 mm long, 4 mm wide; nodules mostly 0.25-0.5 mm in diameter, spaced (tip to tip) 0.35-0.8 mm apart transversely; larger nodules, in whorls, 0.5-1 mm in diameter; collar 0.5-1 mm long, typically less than 1.1 times wider proximally than distally; milled ring only slightly wider than proximal end of collar; base 1-1.5 mm long, 1.2-1.5 times wider distally than proximally.

Table 6. — Measurements of tests of *Eucidaris madrugensis* examined.

Characters	USNM 328221a	USNM 328221b	USNM 328221c	ANSP 50975
(in mm)				
HD	29	27.5 _e	26 _e	25 _e
VD	17	15	14.5	14
PerD	11	14.5	12 _e	—
ApSD	14	14.5	10.5 _e	—
IAmW	13.5	13	12	11.5
AmW	3.5	3.4	3	2.4
IAmPIW	7.6	7.5	6.1	6.5
ArW	5.4	5	4	4.2
MAW	1.4	1.5	1.3	1.5
AdrAW	0.8	1	0.8	0.8
PorAW	0.8	0.9	0.7	0.7
IPorAW	1.6	1.6	1.4	1
(as percentages)				
VD/HD	58	56 _e	56 _e	56 _e
AmW/IAmW	26	26	25	21
ArW/IAmPIW	71	67	66	65
MAW/IAmPIW	19	20	21	23
(as numbers)				
IAmPl:Col	6-7	6-7	7	6-7
AmPl:IAmPl	10	9	8-9	8
IPorTub:AmPl	M+1	M+1	M+1	M+0
_e = estimate.				

Subfamily RHABDOCIDARINAE Lambert

Genus PRIONOCIDARIS A. Agassiz

Prionocidaris cojimarensis (Lambert
and Sánchez Roig in Sánchez Roig)

Plate 4, figures 11-13;
Plate 5, figures 1-12;
Plate 6, figures 1-6

1926. *Cidaris cojimarensis* Lambert and Sánchez Roig in Sánchez Roig, p. 32, pl. 3, fig. 3.
 1930. *Leiocidaris cojimarensis* (Lambert and Sánchez Roig), Lambert and Sánchez Roig, p. 144.
 1949. *Leiocidaris cojimarensis* (Lambert and Sánchez Roig), Sánchez Roig, p. 31.
 1963. ?*Phyllacanthus* sp. Gordon, p. 631, pl. 79, fig. 1.

Description. — Test small to medium size (maximum known HD 33 mm). Vertical diameter little more than half horizontal diameter. Apical system slightly larger than peristome. Ambulacra nearly straight and about one-third as wide as interambulacra. Nine ambulacral plates adjoining interambulacral plate at ambitus in smallest known specimen, 11 to 12 in largest. Poriferous areas slightly depressed. Pores about equal in size, widely spaced, and conjugate.

Interporiferous area 1.2 to 2 times as wide as one poriferous area. Marginal tubercles in regular series with those on adjoining plates; inner area of each plate with one to three smaller inner tubercles.

Eight interambulacral plates per column in largest known specimens. Areoles, occupying 52 to 63 per cent of width of plate, not depressed; those on basicoronal plates confluent in most specimens but separated by some scrobicular tubercles in two (MCZ 4104, USNM 232509). Primary tubercles large, high, perforate; plate-forms narrow and smooth or (in MCZ 4104) crenulate along upper edge on adapical plates. Scrobicular tubercles round to oval, separated by one to several small tubercles or ridge. Plates otherwise covered with small, closely spaced tubercles, these decreasing in size to sutures; tubercles rarely, and then only slightly, aligned in horizontal rows. Median suture slightly depressed.

Radioles small (probably not more than 25 mm long and 4.5 mm wide; usually smaller) and variable. Typically either short and fusiform or longer, more slender and gradually tapered, each type bearing both spinules and small nodules. Another form bearing only small nodules. A third, ridged form is described below. Tips missing in most specimens examined; those present either finely coronate, rimmed by small spinules that are longer on adapical margin, or simply acute. Shaft with as many as 35 irregular series of small nodules or low spinules, these smallest on adoral surface of radiole. Interspersed among small protuberances on one-third to one-half of these series are larger spinules projecting 1.5 mm or less, commonly in three to seven indistinct to distinct whorls. Large spinules not much compressed, but bases of adjoining spinules occasionally joined. Surface between and up sides of nodules and spinules covered with minute nodules (most 0.04 mm in diameter), apparently remnants of hair coat; evidence of anastomosed hairs apparent on a few specimens. Some radioles having short necks. Collars no longer than 2 mm and usually shorter; either scarcely widened proximally or narrowed toward milled ring. Milled ring not prominent. Base commonly about 1 mm long, 1.05 to 1.5 times wider distally than proximally. Acetabular edge usually smooth but in some specimens having faint crenulations along one side.

Radioles apparently of transitional type (intermediate between ambital and oral radioles) found with typical radioles short; tips blunt or slightly widened and fluted, commonly slightly indented,

slightly oblique. Shaft covered by nodules or low spinules, these largest on lateral and adapical surfaces. Minute nodules (hair coat remnants ?) on some specimens. Collars 1 mm long or less.

Oral radioles with tips only slightly, if at all, widened but slightly fluted and indented. Adapical and lateral surfaces of shaft having low nodules; oral surface smooth. Collar up to 2 mm long. One specimen, entirely smooth with slightly produced lateral ridges and slightly indented tip, may be oral radiole forming by regeneration like those noted previously (Cutress, 1965) in *Eucidaris tribuloides*.

Third form of apparent ambital radiole, although at outer range of variability so different from typical radioles of *P. cojimarensis* that it appears to belong to a different species, intergrades to typical form. These radioles up to 25 mm long and 3 mm wide. Shafts having 10 to 14 distinct longitudinal ridges, these commonly dentate or crenate proximally, dentate or serrate through middle portion, and smooth near tip. Midshaft protuberances more or less uniform in size or variable; if the latter, several whorls of larger but low serrations may be present. Grooves and sides of ridges in well preserved specimens covered by minute granules up to 0.04 mm in diameter. Collars in known specimens as long as 1 mm but usually less and very little widened proximally. Milled rings only slightly wider than proximal end of collar. Bases commonly longer than collar but not more than 1 mm long and 1.2 to 1.3 times wider distally than proximally. Acetabula smooth.

Similar but slightly different, very small radioles, collected by Dr. P. J. Bermúdez in Dominican Republic and Trinidad, questionably referred to species; these not more than 10 mm long, 2 mm wide, fusiform to cylindrical. Shafts with seven to 13 serrate ridges or straight series of peaked nodules or low spinules, these in some radioles slightly larger in one or, more rarely, two indistinct transverse whorls on lateral and adapical surfaces. Surface otherwise covered by minute nodules or possible remnants of anastomosed hairs. Collars usually less than 0.5 mm long. Bases also less than 0.5 mm but longer than collar in some specimens. Faint crenulations along adapical edge of most undamaged acetabula. All radioles in one lot (PRI 29734) compressed to some extent; some completely flat, including collar, milled ring and base, flattening that apparently

occurred during fossilization but after radioles had somehow softened; no cracking of specimens apparent such as would be expected if pressure were applied to hard calcite.

Discussion. — *Cidaris cojimarensis* was named by Lambert and Sánchez Roig from a single radiole described as 18 mm long, 2.5 mm wide, with coronate tip and longitudinal series of unequal "granulitos," some more projecting than others; it was said to recall radioles of *Cidaris lutkeni* Loriol (= *Prionocidaris bispinosa* (Lamarck)), according to those authors), only less spinulose. Such a radiole would fit well into the series of radioles here referred to *P. cojimarensis*.

Lambert in Sánchez Roig, (1949, p. 31) subsequently gave a diagnosis of the species based on a 17 mm wide fragment from the lower part of a small test; it was described as having straight ambulacra with four rows of granules, wide interambulacral plates, areoles of the first adoral plates confluent but others separated by a line of granules, median area moderately wide, adradial area narrow, secondary nodules closely spaced but not aligned. Because Lambert referred the species to *Leiocidaris*, I assume the test fragment had conjugate pores. In all these features, the test specimens here referred to *P. cojimarensis* agree well with Lambert's test fragment.

There are a few discontinuities in the series of test measurements recorded in Table 7. USNM 232507 and 232509 have fewer interambulacral plates per column than expected, and UCMP 14427 has too few ambulacral plates per interambulacral plate to give a smooth progression from small to large specimens. Yet, series of test measurements of Recent *Prionocidaris verticillata* (Lamarck) from the Indo-Pacific region and some other Recent *Prionocidaris* species (see Appendix) show variabilities of similar sort and magnitude.

The Gordon test fragment (USNM 647834) has scrobicular tubercles more like those in *Prionocidaris* than *Phyllacanthus*; its pores are distinctly conjugate. It is like smaller test fragments collected by C. W. Cooke in the Cibao marls of Puerto Rico from which Cooke also collected radioles similar to sparsely spinulose *P. cojimarensis* radioles from Cuba. The Gordon specimen, therefore, is referred to this species. The possibility can not be overlooked, however, particularly because it is from a larger test (possibly near 40 mm HD) than the Cooke tests, that the Gordon specimen might belong to a new species of *Prionocidaris* to which two other Puerto Rican radiole fragments are here referred.

The Cuban radioles here referred to *P. cojimarensis* are very variable. Even the typical form ranges from more or less evenly spinulose to distinctly verticillate. Intermediate examples intergrade from both simply nodulose and distinctly ridged forms into the typical form. Nodulose and ridged forms occur together with the typical form at a large proportion of known Cuban *P. cojimarensis* localities, a further indication that the three forms are conspecific. The distribution of the ridged form is especially striking; it was found in eight of the 13 Cuban localities, always with the typical form.

The extreme variability of radioles in *P. cojimarensis* is not unique; it is apparent in other prionocidarid fossil species discussed on following pages and is nearly equaled in *Prionocidaris baculosa* (Lamarck), now living in the Indo-Pacific region. Typical radioles in the Recent species are relatively short, columnar, uniformly dark, ornamented with closely spaced, uniform, low spinules and have collars that are not more than 2 mm long. Some of the radioles of *P. baculosa* "var." *annulifera* H. L. Clark are large, tapered, ringed in red and white, and have prominent, serrate, lateral keels, one to three prominent, longitudinal rows of spinules on the adapical surface, and collars commonly about 3 mm long. There is considerable variability within the two forms of radioles and intermediate examples, but the extremes are so different that, viewed together without intergrades, they seem to represent different species. In *P. baculosa*, as in *P. cojimarensis*, there is a third form of radiole, like the typical form but with a few laterally compressed spinules.

P. cojimarensis differs from *Prionocidaris spinidentatus* (Palmer in Sánchez Roig, which also lived in the Caribbean during the Miocene, in its smaller size, greater ambulacral width/interambulacral width ratios, fewer interporiferous tubercles on its test and smaller, commonly whorled spinules on its radioles. It differs markedly also from *Prionocidaris cookei* Cutress, a Florida Miocene species that also lived in the Cuban Miocene. *P. cookei* has larger areoles and narrower median areas (compared to plate width) and radioles bearing smaller spinules that are not arranged in whorls.

P. cojimarensis is more similar to two other Caribbean species, *Prionocidaris clevei* (Cotteau) of early Miocene age and the new species of *Prionocidaris* from early to middle (?late) Miocene time.

In discussions of the latter two species, differences between them and *P. cojimarensis* are detailed. *P. cojimarensis* also resembles the Recent species *Prionocidaris verticillata* (Lamarck) from the Indo-Pacific region, but in the latter the radioles are not polytypic and the spinules are always in whorls that are more distinct than in most of the *P. cojimarensis* radioles.

P. cojimarensis most closely resembles *Prionocidaris praeverticillata* Stephenson (1968, p. 511) from the Baratuma Beds of Kenya and Gáj Series of western Sind (Pakistan), both dated early Miocene. On the basis of extant material, however, *P. cojimarensis* appears to be a distinct, smaller species.

Of seven test fragments of *P. praeverticillata* examined (HM E1265/1-3; Sedgwick C59503-4, C59551, C76304), three appear to have been ambital in position and thus of value for comparison with the *P. cojimarensis* records in Table 7. These three plates are 12.5 to 15 mm wide, and one (C59503) has 17 ambulacral plates adjoining it; the largest ambital interambulacral plate known for *P. cojimarensis* is 12 mm wide and has 13 ambulacral plates attached to it. Ambulacral plates of *P. praeverticillata* have marginals plus two to three inner tubercles. Almost all such plates in *P. cojimarensis* have one to two inner tubercles (only in USNM 232509 is there a third). These differences may be size-related. However, a 22 per cent ambulacral width/interambulacral width ratio in the only *P. praeverticillata* specimen (Sedgwick C59503) where this could be estimated, contrasted to the 27 to 36 per cent range for this ratio in *P. cojimarensis*, strongly suggests the two species are distinct.

The radioles, of which there are sizeable samples for both species, also indicate that *P. cojimarensis* stands apart from *P. praeverticillata*. Most of the radiole specimens of both species are incomplete, so no close comparison of length is possible, but widths indicate the radioles of *P. cojimarensis*, on the whole, are the smallest. Of 38 *P. praeverticillata* fragments examined (HM E1304-9, E1487/3-4, E1487/7-11; Sedgwick C59482-83, C59588-97; casts of GSI types 2719, 2720, 2734, 2740; and 10 specimens in the personal collection of D. G. Stephenson, Department of Geology, University of Keele), the maximum widths were: 2 mm in one specimen, 3 to 3.9 mm in seven, 4 to 4.9 mm in 12, and 5 to 6.8 mm in

the other 18. In a measured group of 61 *P. cojimarensis* radiole fragments, including the largest and best preserved in lots PRI 29655-8, 29660, 29662-3, 51 have maximum widths of less than 3 mm, 10 reach 3 to 3.9 mm, and none are wider. In *P. praeverticillata* radioles, the large spinules in whorls project as much as 2.5 mm although more commonly this value is nearer 1 mm; in *P. cojimarensis*, maximum projection of large spinules is 1.5 mm and usually less than 1 mm.

On the other hand, despite their being generally more slender, the radioles of *P. cojimarensis* tend towards greater numbers of longitudinal series of protuberances (nodules and interspersed spinules). In the 38 *P. praeverticillata* radioles, 31 have 11 to 19 series, and seven have 20 to 29. In 43 *P. cojimarensis* specimens sufficiently well preserved to count the series of nodules, three have fewer than 10 series, 16 have 11 to 19, 21 have 20 to 29, and three have 30 or more.

Certainly *P. cojimarensis* and *P. praeverticillata* are very close, but on the basis of known specimens, they appear to be distinct species. Possible lines of descent, including the two species, are discussed later in this paper.

The serrate-ridged radioles of *P. cojimarensis* closely resemble those of *Cidaris vafellus* Loriol from the Miocene of Angola, although the largest of the *C. vafellus* radioles are about the same size as the smallest of the ridged *P. cojimarensis* radioles from Cuba. There are no other consistent differences. The *C. vafellus* specimens may be a ridged form of radiole of some *Prionocidaris* species, possibly *P. praeverticillata* or a descendant.

The radioles from the Dominican Republic and Trinidad in the Bermúdez collection are all very small. Many have partially crenulate acetabula, indicating they may be from young specimens. On the other hand, there are a few signs of anastomosing hairs, which indicate the radioles are from adult specimens. Also, even though there are well over 100 radioles from nine localities, no larger, typically verticillate *P. cojimarensis* radioles are known from either island. There is some doubt, therefore, that these radioles are conspecific with the Cuban species, but at present there is no better "slot" for them. Three ridged radioles, collected by the USGS in the Dominican Republic, also are questionably referred to *P. cojimarensis* (see "Material").

Stanton (1966, pl. 7, fig. 18) illustrated a fragment of radiole from the upper Miocene of California that had verticillate groups of protuberances, apparently spinules, as distinct as any seen in *P. cojimarensis*, but such scant material does not permit close comparison with the Caribbean species. It is conceivable that stocks of *P. cojimarensis* migrated into the eastern Pacific before closure of the Panamanian isthmus.

Material.—Lambert and Sánchez Roig's radioles (no. 1343) and a test fragment (no. 1383), both designated in Sánchez Roig (1949, p. 31) as "Tipo No. 105, Colección Sánchez Roig," were not available for study.

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez 48	PRI 29653	P. J. Bermúdez	—	1
Bermúdez 48	PRI 29714	P. J. Bermúdez	—	7 _c
Bermúdez 229	PRI 29654	P. J. Bermúdez	1	36
Bermúdez 229	PRI 29715	P. J. Bermúdez	—	7 _c
Bermúdez 230	PRI 29655	P. J. Bermúdez	—	23
Bermúdez 230	PRI 29716	P. J. Bermúdez	—	3 _c
Bermúdez 234	PRI 29656	P. J. Bermúdez	—	16
Bermúdez H-15,262	?PRI 29728	P. J. Bermúdez	—	7 _c
Bermúdez H-15,265	?PRI 29729	P. J. Bermúdez	—	3 _c
Bermúdez H-15,448	?PRI 29730	P. J. Bermúdez	—	2 _c
Bermúdez H-15,462	?PRI 29731	P. J. Bermúdez	—	67 _c
Bermúdez H-15,468	?PRI 29732	P. J. Bermúdez	—	9 _c
Bermúdez H-15,473	?PRI 29733	P. J. Bermúdez	—	3 _c
Bermúdez H-20,093	?PRI 29734	P. J. Bermúdez	—	63 _c
Gordon (a)	USNM 647834	W. A. Gordon	1	—
Palmer 405	MCZ 4103	R. H. Palmer	1	—
Palmer 405	PRI 29657	R. H. Palmer	—	37
Palmer 405	PRI 29717	R. H. Palmer	—	2 _c
Palmer 405A	PRI 29658	R. H. Palmer	—	20
Palmer 405A	PRI 29718	R. H. Palmer	—	3 _c
Palmer 926	PRI 29659	R. H. Palmer	—	9
Palmer 976	MCZ 4104	R. H. Palmer	1	2
Palmer 1018	PRI 29660	R. H. Palmer	1	149
Palmer 1018	PRI 29719	R. H. Palmer	—	56 _c
Palmer 1025 _a	PRI 29662	R. H. Palmer	—	93
Palmer 1025 _a	PRI 29721	R. H. Palmer	—	6 _c
Palmer 1026	PRI 29663	R. H. Palmer	—	62
Palmer 1026	PRI 29723	R. H. Palmer	—	22 _c
Palmer 1026	PRI 29763	R. H. Palmer	—	21
Palmer 1026	PRI 29664	P. J. Bermúdez	—	38
Palmer 1026	PRI 29722	P. J. Bermúdez	—	6
Palmer 1028	PRI 29665	R. H. Palmer	—	1
Palmer 1098	ANSP 50984	R. H. Palmer	1	—
Palmer 1553	PRI 29754	R. H. Palmer	—	5 _c
Palmer 1554	PRI 29727	R. H. Palmer	—	2
Palmer 1635	PRI 29756	R. H. Palmer	—	14 _c
UCMP B-3286 _b	UCMP 14427	R. H. Palmer	1	—
USGS 8583	?USNM 232520	F. W. Penney	—	2 _c
USGS 8727	?USNM 242730	D. D. Condit	—	1 _c

Material. — (continued)

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
USGS 19700	USNM 232507	C. W. Cooke	1	—
USGS 19714	USNM 232508	C. W. Cooke	—	2
USGS 19718	USNM 232509	C. W. Cooke	1	—
USGS 19720	USNM 232510	C. W. Cooke	—	2
USGS 19760	USNM 232511	C. W. Cooke	—	1
USGS 19837	USNM 232512	C. W. Cooke	—	1

^a = near type-locality, ^b = equivalent of Palmer locality 405, ^c = includes ridged form of radiole, ? = questionably referred to species.

Stratigraphic occurrence and localities. — lower to middle (or possibly upper) Miocene (Cojímar Formation) and middle Miocene (Güines Formation, upper and lower Yumurí limestone), Cuba; upper lower or middle Miocene possible to Pliocene (Cibao limestone), Puerto Rico. Possibly also upper Miocene to Pliocene (Gurabo Formation), Dominican Republic; and Trinidad, strata not specified.

Measurements. — See Table 7 for test measurements. Typical and simply nodulose radioles: length probably 25 mm at maximum but commonly 20 mm or less; width 4.5 mm at maximum but usually 1.5-2.5 mm; nodules or low spinules on shaft 0.15-0.8 mm in diameter, longer than wide and smaller on adoral surface; larger spinules 0.4-1.5 mm wide and projecting 0.3-1.5 mm; most minute nodules (remnants of hair coat?) 0.04 mm but a few up to 0.08 mm in diameter; neck, if present, 0.3-1.6 mm long; collar usually 1-1.5 mm long but ranging from 0.4-2 mm, nearly same width throughout; base commonly about 1 mm long but ranging from 0.4-1.8 mm and 1.05-1.5 times wider distally than proximally.

Ridged radioles: maximum length probably near 25 mm; width of known specimens 3.5 mm at maximum but commonly less; ridges 0.15 to 0.55 mm wide, projecting not more than 0.55 mm; minute (hair?) nodules, 0.04 mm wide or smaller; collar 0.25 to 0.55 mm long, 0.05 to 0.1 mm wider proximally than distally; milled ring 0.05 to 0.15 mm wider than proximal collar; base 0.5 to 1 mm long, 0.1 to 0.4 mm narrower proximally than distally.

Prionocidaris spinidentatus (Palmer
in Sánchez Roig)

Plate 7, figures 1-8;
Plate 8, figures 1-5;
Plate 9, figures 1-3

1902. ?*Cidaris avenionensis* Desmoulins, Lovisato, p. 12.

1902. ?*Leiocidaris sismondai* K. Mayer, Lovisato, p. 12.

Table 7. — Measurements of test specimens of *Prionocidaris cojimarensis*.

Characters	USNM 647834	ANSP 50984	MCZ 4104	UCMP 14427	PRI 29660	USNM 232507	USNM 232509	MCZ 4103
(in mm)								
HD	—	33 _e	30 _e	28 _e	—	28 _e	28 _e	22 _e
VD	—	18	18 _e	15 _e	—	15 _e	13	10 _e
PerD	—	—	—	—	—	—	12 _e	9 _e
ApSD	—	—	—	—	—	—	14 _e	11 _e
lAmW	22 _e	18	14 _e	13.5 _e	13.4 _e	12	12	10
AmW	6	5.3	5	4.3 _e	4.2 _e	4	4	3
lAmPlW	12	10	9	7.9	7.4	6.3	7	5.7
ArW	7	5.2	5	4.3	4.2	4	4	3.2
MAW	3.5	2.8	2.5	2.1	2.2	1.7	1.8	1.4
AdrAW	2	2.2	1.5	1.2	1.3	0.6	1.2	0.8
PorAW	1.5	1.6	1.3	1.2	1.1	1	1	0.7
lPorAW	3	1.9	2.4	1.9	2	2	2	1.8
(as percentages)								
VD/HD	—	55 _e	60 _e	54 _e	—	54 _e	46 _e	45 _e
AmW/lAmW	27 _e	30	36 _e	32 _e	31 _e	33	33	30
ArW/lAmPlW	58	52	56	58	54	63	57	61
MAW/lAmPlW	29	28	28	26	29	27	26	25
(as numbers)								
lAmPl:Col	—	8	7	7	—	6-7	6-7	7
AmPl:lAmPl	13 _e	11	11-12	9-10	11	11	10	9
lPorTub:AmPl	M+1-2	M+1-2	M+1-2	M+1	M+2	M+1-2	M+1-3	M+1

_e = estimate.

1922. *Cidaris* sp. b. Jackson, p. 19, text figs. 2-3.
1949. *Leiocidaris spinidentatus* Palmer in Sánchez Roig, p. 32, pl. 1, fig. 3.
1949. ?*Goniocidaris holguinensis* Sánchez Roig, p. 31.
1949. ?*Goniocidaris holguenensis* [sic] Sánchez Roig, Brodermann Vignier, p. 322.
1974a. ?*Prionocidaris* sp. Brito and Ramires, p. 266, pl. 1, fig. 4, pl. 4, fig. 4.

Description.—Test large, high. Largest known fragment from individual of about 80 mm horizontal diameter and 65 mm vertical diameter. Adapical surface flattened. Apical system apparently smaller than peristome. Ambulacra almost straight, about one-fifth width of interambulacra in large specimens but nearer one-third in smallest specimen. Twelve ambulacral plates adjoining interambulacral plate at ambitus in large specimens. Poriferous areas only slightly depressed. Pores oval, widely spaced, distinctly conjugate; horizontal ridge along top of plate very narrow. Interporiferous area twice as wide as one poriferous area. Marginal tubercles in regular series with those on adjoining plates. Up to four to six inner tubercles per plate, these more or less equal in size but not more than half as large as marginals; arranged in single row in smallest specimen but in irregular double row in largest.

Twelve to 13 interambulacral plates per column in largest known specimen. Areoles relatively large in young specimens but, due to their lower growth rate compared to that of median and adradial areas, appearing small in large specimens; only slightly depressed; all separated by at least a few scrobicular tubercles, even on adoral plates. Primary tubercles large but only moderately high; platforms either entirely smooth or having faint crenulations along upper margin; mamelon perforate. Scrobicular tubercles inconspicuous in largest specimen because of large size of plates but actually large; edges nearly contiguous or separated by small ridge; inner edge canted toward scrobicule; outer edge not raised but clearly marked. Median and adradial areas covered by small tubercles, these in large specimens aligned in horizontal rows separated by distinct grooves. Median areas in largest specimen unusually wide, wider than areole.

Matching of radiole fragments according to taper and ornamentation indicates typical radioles were probably at least 65 mm long but not more than horizontal diameter of known tests. Radioles stout (up to 6.8 mm wide), straight, tapered, almost always slightly flattened distally, commonly grossly spinulose. Most known tips

coronate, either rimmed by large, compressed spinules or having nearly entire, smooth edges; adapical edge longer than adoral so that tip is oblique. Radioles probably from adapical plates shorter, most with type of coronate tip having entire margin. Shafts usually having six to eight irregular longitudinal series of large spinules, these largest on lateral and adapical surfaces; a few having only two lateral series of spinules. Spinules projecting as much as 5 mm, either perpendicular to surface or inclined somewhat distally; sometimes hooked; some of those on proximal portion of shaft vertically compressed, others obviously compound with saw-toothed tips; not arranged in distinct tranverse whorls; lacking on adoral surface of some radioles. Shaft otherwise, in many well-preserved specimens, covered with small, rounded or peaked nodules or low spinules in up to 50 irregular series and, overall, with minute, closely spaced nodules, probably remnants of hair coat. Collars short, rarely up to 4 mm long; slightly widened to slightly narrowed proximally. Milled ring very little wider than proximal end of collar. Base up to about 2 mm long, distinctly narrowed proximally. Acetabular edge on some radioles smooth, on others showing faint crenulations along one half.

Transitional and oral radioles shorter and bearing small spinules, these limited to adapical and lateral surfaces. Tips fluted, oblique, and indented at end but only slightly, if at all, widened. Secondary spines unknown.

As in *Prionocidaris cojimarensis*, two other forms of radioles are apparent in *Prionocidaris spinidentatus*. In one, shafts lacking large spinules and covered only with small and minute nodules. Another form spinulose but distinctly ridged. Largest of the latter more grossly spinulose than any of ridged radioles of *P. cojimarensis*. Largest complete ridged radiole 27 mm long, 3.5 mm wide, but some known fragments appear to be from longer radioles. Shafts with 10 to 15 longitudinal, serrate, dentate or crenate ridges, four to seven of these (on adoral surface) narrower and more closely spaced than those on sides and upper surface. Lateral ridges particularly prominent, almost wing-like in some specimens. Interspersed along adapical ridges are larger serrations or spinules, commonly discrete, largest projecting 1.2 mm. On a few specimens, largest protuberances in one to three faint whorls on proximal shaft. On distal, tapered part of radiole, ridges not fewer in number but narrower and more closely spaced and, on some specimens, almost smooth. Minute

granules, between and up sides of ridges, joined into ridges. Very narrow, dark, bare area above collar on some radioles, otherwise no neck. Collars up to 1.3 mm long, only slightly widened proximally. Bases about same length as collar and 1.2 to 1.5 times wider distally than proximally. Ridged radioles known from three of known *P. spinidentatus* localities, two (Palmer locs. 1042 and 1454) in Cuba, one (Cutress loc. 2) in Puerto Rico, always found in association with typical form of radiole.

Discussion. — The species *Leiocidaris spinidentatus*, credited to R. H. Palmer by Sánchez Roig (1949, p. 32), was based on radioles collected in Cuba by Dr. Palmer. No description was given, but an illustration of one of the radioles (Sánchez Roig, 1949, pl. 1, fig. 3) shows what the species is; oriented base upwards in the illustration, this specimen is clearly conspecific with many other spinulose radioles collected by Palmer and Dr. Pedro J. Bermúdez in Cuba and now located in the ANSP, MCZ, PRI and UCMP collections.

A test capable of supporting the long, stout radioles of *Prionocidaris spinidentatus* would need to be large. Fragments collected at several localities where *P. spinidentatus* radioles occur are from large tests, appear to be referable to *Prionocidaris*, and therefore are assigned to the same species. We are thus able to delineate the species more precisely.

Goniocidaris holguinensis Sánchez Roig (1949, p. 31) may be identical to *P. spinidentatus*. The *G. holguinensis* radioles were collected by Dr. Palmer. The locality given by Dr. Sánchez Roig, although not cited by number, coincides exactly with Palmer locality 1042, where many of Palmer's *P. spinidentatus* radioles were collected. However, although the *G. holguinensis* radioles were described as having hooked spinules 3 to 5 mm long, as in *P. spinidentatus*, they also were described as verticillate, and the spinules on *P. spinidentatus* radioles are almost never in distinct whorls. Also, Sánchez Roig made no reference to similarities between *G. holguinensis* and *P. spinidentatus* even though he apparently had seen specimens of both, and indeed it would be strange if he described as a new species, in the same paper and only one page ahead, specimens that were the same as Palmer's species. If at some future date *P. spinidentatus* and *G. holguinensis* are proved conspecific, the first reviser would be justified, under provisions of Article 24A of the

"International Code of Zoological Nomenclature," in selecting *spinidentatus* as the specific name having priority. It is descriptive of the radioles, its first use in publication was accompanied by an illustration sufficient to characterize the radioles, and there is a wealth of material that is identifiable as species *L. spinidentatus*.

It is not certain from the figures of *Prionocidaris* sp. Brito and Ramires (1974a, pl. 1, fig. 4; pl. 4, fig. 4) from the upper Miocene (Pirabas Formation) of Brazil whether this species belongs with *P. spinidentatus*. Only three or four of the illustrated radiole fragments are similar to some *P. spinidentatus* radioles. Much of the Brazilian test is encrusted with bryozoans and polychaete tubes, and the illustration otherwise does not permit close comparison of the specimen with the Cuban test fragments here assigned to *P. spinidentatus*. It appears, however, to be part of a test that is smaller than the Cuban specimens.

P. spinidentatus is easily distinguished from the four other species of *Prionocidaris* known from the Caribbean Miocene, *P. cojimarensis*, *P. cookei*, *P. clevei* and a new species. It is a much larger species with more grossly spinulose radioles than the first three. Its radioles are not verticillate, as they are in all the others except *P. cookei*. It has narrower ambulacra, more interporiferous tubercles, and a higher median area width/interambulacral width ratio, at least in large specimens, than the other four. It stands closest to the new species of *Prionocidaris*; differences between the two are discussed under that species.

The test of *P. spinidentatus* shows considerable similarity to that of *Cidaris adamsi* Wright (1864, p. 474, pl. 21, fig. 5) from the Aquitanian of Malta and *Cidaris* sp. Duncan and Sladen (1882-1886, p. 250, pl. 39, figs. 1-2) from the Nari Series of western Sind (Pakistan). I examined Wright's specimen (BM E1868) and found it different from *P. spinidentatus* in having greater areole width with respect to plate width, in having the four to six inner tubercles on the ambulacral plates arranged more distinctly in two (upper and lower) rows, and in lacking the faint crenulations on the upper margin of adoral tubercles seen in some specimens of *P. spinidentatus*. Wright (1864, p. 475) indicated that *C. adamsi* was collected by Leith Adams from Adams' Bed 5 (Miocene) in Malta. Fragments of spinulose radioles (BM E43350-92) that, according to data with the specimens, were taken from the same bed may be conspecific

with *C. adamsi*. These radioles differ in important respects from those of *P. spinidentatus*: they have shorter collars (1 to 1.5 mm long), wider tips (BM E43351 flares to 25 mm!) and many laterally compressed spinules. In the last respect, these radioles are more like those of *Chondrocidaris gigantea* (A. Agassiz), which lives in the Indo-Pacific.

Other Miocene tests and spinulose radioles resembling those of *P. spinidentatus* include *Goniocidaris* sp. a Duncan and Sladen (1883, p. 53, pl. 8, figs. 11, 13-14) from the Arenaceous series of Kachh; *Phyllacanthus sundaica* Martin (1883-1887, p. 287, pl. 15, figs. 293e-g) from the Tertiary of Java; *Cidaris avenionensis* Desmoulins (Gregory, 1891, p. 587, pl. 1, fig. 1c; these specimens are from the *Globigerina* limestones (lower Miocene) of Malta but the species is recorded by Gregory from other Tethyan localities); *Leiocidaris sismondai* Mayer (Lambert, 1907-1909, p. 19, pl. 1, fig. 1-6); and *Cidaris lovisatoi* Cotteau (1895, p. 7) from Sardinia.*

In Lovisato's (1902) paper on the fossils from the "calcare compatto" of Bonaire and Saint Bartholomew, *Cidaris avenionensis* Desmoulins and *Leiocidaris sismondai* K. Mayer were listed (p. 12) but not illustrated. Because these two Mediterranean-area species are similar to *P. spinidentatus*, the Lovisato specimens likely are conspecific with the specimens here referred to that species.

P. spinidentatus is also very similar to *Prionocidaris bispinosa*, now living in Australian and Indo-Pacific seas. Radioles in both species are polytypic, some lacking the large spinules, but in *P. bispinosa* the maximum size of the small nodules on the shafts is considerably less (0.25 mm) than in the fossil, and the collars are longer (5 to 7 mm); transverse alignment of the large spinules into whorls is common in *P. bispinosa* but very rare in the fossil; and the edges

*A copy of the following article was received after my paper went to press:

Zammit-Maempel, G.

1979. *The Indo-Pacific affinity of some Maltese Tertiary fossils*. Cent. Mediterr. Nat., vol. 1, No. 1, pp. 1-12.

Six cidaroids, all previously assigned to *Cidaris*, were reassigned generically: *Cidaris melitensis* Wright to *Stylocidaris*; *Cidaris adamsi* Wright, *Cidaris scillae* Wright and *Cidaris oligocenus* Gregory to *Phyllacanthus*; and *Cidaris sismondai* Mayer and *Cidaris avenionensis* Desmoulins to *Prionocidaris*. Three of these species are mentioned above, and *C. melitensis* is included in the discussion of *Tretocidaris anguillensis*.

of the coronate tips in *P. bispinosa* are almost never entire as they are in *P. spinidentatus*.

Tests of the two species also show a few differences. In *P. spinidentatus*, the vertical diameter of the test is greater than in *P. bispinosa*, there are fewer ambulacral plates adjoining an interambulacral plate at the ambitus, there are more inner ambulacral tubercles, and the peristome apparently is a little larger than the apical system instead of the reverse, as in *P. bispinosa* (compare measurements of *P. spinidentatus* in Table 8 with those for *P. bispinosa* of comparable size in the Appendix).

Chondrocidaris gigantea, another Recent Indo-Pacific species, has a large test, exceptionally wide interambulacral plates, smooth tubercles, and subconjugate pores. With respect to ambulacral width, relative widths of apical system and peristome, number of inner tubercles on ambulacral plates, and lack of small nodules on many of the radioles, *P. spinidentatus* is nearer *C. gigantea* than *P. bispinosa* (see Table 8 and Appendix). However, in *P. spinidentatus*, the small tubercles on the median areas of interambulacral plates do not appear to be like the glassy knobs with spine attachment points at the side that are typical of *Chondrocidaris*. Also, the radioles of *P. spinidentatus* are very much more like those of *P. bispinosa* in having flaring, coronate tips, spinules that, if compressed, are flattened in the transverse plane, and shafts of some specimens that are simply nodulose, lacking spinules.

The bathymetric ranges of Recent species of *Prionocidaris* indicate that *P. spinidentatus* may have lived in deep water. However, this Miocene species has been collected in some of the same localities as *Phyllacanthus peloria* (Jackson), and modern *Phyllacanthus* species are usually littoral.

Material.—The holotype (specimen 106 in the Sánchez Roig collection) was not seen.

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez (b)	PRI 29673	P. J. Bermúdez	—	57 _b
Cutress 2	PRI 29755	E. Ortiz-Corps	—	5
Palmer (a)	MCZ 4108	R. H. Palmer	—	7 _l
Palmer 75	PRI 29674	P. J. Bermúdez	—	11
Palmer 1028	PRI 29756	P. J. Bermúdez	—	10
Palmer 1040	PRI 29675	R. H. Palmer	—	2 _b
Palmer 1041	PRI 29676	R. H. Palmer	—	12 _l
Palmer 1042	ANSP 50977	R. H. Palmer	1	2 _b

Material. — (continued)

Locality	Catalogue Number	Collector	Numebr of specimens	
			Test	Radiole
Palmer 1042	ANSP 50978	R. H. Palmer	—	11
Palmer 1042	ANSP 50985	R. H. Palmer	—	2 _c
Palmer 1042	PRI 29677	R. H. Palmer	—	42
Palmer 1042	PRI 29678	P. J. Bermúdez	—	6
Palmer 1056	PRI 29724	R. H. Palmer	—	1 _c
Palmer 1107	PRI 29680	R. H. Palmer	—	36
Palmer 1262	PRI 29725	P. J. Bermúdez	—	1
Palmer 1320	PRI 29681	R. H. Palmer	—	2
Palmer 1452 _a	ANSP 50980	R. H. Palmer	1	—
Palmer 1452 _a	ANSP 50981	R. H. Palmer	—	6
Palmer 1452 _a	PRI 29682	R. H. Palmer	—	211
Palmer 1452 _a	PRI 29726	R. H. Palmer	—	53 _c
Palmer 1626	ANSP 50982	R. H. Palmer	4	—
Palmer 1627	PRI 29683	R. H. Palmer	—	10
Palmer 1719	PRI 29684	R. H. Palmer	—	3
UCMP B-3493	UCMP 14428-14432	R. H. Palmer	—	5
USGS 20	USNM 328282	W. R. Forest	1	—
USGS 44	USNM 232514	W. R. Forest	1	5

_a = type-locality, _b = includes nodulose form of radiole, _c = includes ridged form of radiole.

Stratigraphic occurrence and localities. — lower to upper Oligocene(?) and Miocene (horizon not indicated), Cuba; lower Miocene (Antigua Formation), Antigua; middle (or possibly lower) Miocene to Pliocene (Ponce Formation), Puerto Rico.

Measurements. — See Table 8 for measurements of the most complete test specimens. Radioles: maximum length of ambital radiole 65 mm or more but probably not more than HD of test; width 6.8 mm at maximum, more commonly 4-6 mm; spinules projecting as much as 5 mm, up to 4 mm in basal diameter; nodules on shaft usually 0.15-0.5 mm, rarely up to 0.7 mm, in diameter; minute nodules (remnants of hair coat?) 0.08-0.15 mm in diameter; neck, if present, 0.5-1 mm long; collar commonly 2-3 mm, rarely 4 mm, long, of uniform width throughout or slightly narrower proximally in some specimens, but usually 1.1-1.3 times wider proximally than distally; milled ring typically no more than 0.1-0.2 mm wider than proximal collar; base commonly 1.6-2.1 mm long and 1.3-1.9 times wider distally than proximally.

Prionocidaris katherinae, new species

Plate 9, figures 4-10

1922. *Cidaris* sp. b, Jackson, p. 19, text-fig. 2-3.

Diagnosis. — Radioles up to 5.5 mm wide, with five or more transverse whorls, one row wide, of large, laterally compressed

Table 8.—Measurements of test specimens of *Prionocidaris spinidentatus*.

Characters	USNM 232514	ANSP 50977	ANSP 50980 (topotype)	USNM 323282	ANSP 50982
(in mm)					
HD	83.	75.	—	65.	30.
VD	66.	—	—	—	—
PerD	40.	—	—	—	—
ApSD	35.	—	—	—	—
IAmW	52	36.	—	—	17
AmW	10	8.	—	—	5.1
IAmPIW	29	19	19	16	8.5
ArW	10	9	8.5	8.5	5.5
MAW	12	6	7.5	5	1.7
AdrAW	7	4	3	2.5	1.3
PorAW	3	2.3	—	—	1.3
IPorAW	6	3.4	—	—	2.6
(as percentages)					
VD/HD	80.	—	—	—	—
AmW/IAmW	19	22.	—	—	30
ArW/IAmPIW	34	47	45	53	65
MAW/IAmPIW	41	32	39	31	20
(as numbers)					
IAmPI:Col	12-13	—	—	—	—
AmPI:IAmPI	12	11	12	—	10
IPorTub:AmPI	M+4-6	M+2-3	—	—	M+4-6

. = estimate.

spinules, these projecting as much as 3.5 mm. Surface of shaft otherwise with up to 25 series small, peaked nodules and minute (hair coat?) nodules.

Description.— Only known test fragment, an interambulacrum with adjoining half ambulacrum, from medium-sized test with vertical diameter scarcely more than half estimated horizontal diameter. Ambulacra almost straight and 30 per cent width of interambulacra. Ten ambulacral plates per interambulacral plate at ambitus. Pores about equal in size, spaced about two pore widths apart, subconjugate; upper ridge thick, groove at lower edge of plate narrow. Interporiferous area only slightly wider than one poriferous area. Marginal tubercles in regular series with those on adjoining plates; one or, occasionally, two smaller tubercles inside marginals on each plate.

Seven to eight interambulacral plates per column. Areole width 61 per cent of plate width; areoles on basicoronal plates confluent. Primary tubercles large, perforate, and smooth. Scrobicular tubercles

round, separated by small tubercle or ridge. Outside scrobicular ring, small tubercles decreasing slightly in size toward sutures.

One nearly complete radiole, possible from adapical position on test, 34 mm long (before being cut for transverse section), 5.4 mm at widest and slightly flattened distally. Tip (partly chipped) slightly widened and coronate. Most other specimens fragmental. Some, although only 3 to 4 mm wide, apparently from longer radioles; shaft of most at least slightly flattened. Widest of these fragments with up to five (probably more on complete radiole) distinct, transverse whorls of large, laterally compressed spinules, these projecting as much as 3.5 mm; single row of six to 10 spinules per whorl. Shaft otherwise having up to 25 longitudinal series of small, peaked nodules; minute nodules, probably remnants of a hair coat between and up sides of other protuberances. Collars up to 2.5 mm long, only slightly widened proximally. Milled ring slightly wider than proximal end of collar. Bases up to 2 mm long, 1.2 to 1.5 times wider distally than proximally. Several of smallest radioles with faint indications of crenulations on one side of acetabulum.

Prionocidaris katherinae apparently also has ridged radioles, these smaller than whorled form and possibly from young individuals. Best preserved specimen (PRI 29720 from Palmer loc. 1024) 12 mm long, lacking tip, 2.5 mm wide, with 10 longitudinal, crenate ridges. Other specimens (PRI 29746 from Palmer loc. 997) all lacking cortex; subcortical ridges evident on some, a few with faint indications of one or two whorls of small, compressed spinules; dimensions of largest comparable to those of specimen from Palmer locality 1024.

Fragments from Palmer locality 813, most poorly preserved, referred only questionably to species. If correctly referred, one radiole having only nodules on shaft (PRI 29751) suggests third radiole form in *P. katherinae* similar to that in two previously discussed prionocidarid species.

Discussion. — In shaft width and length of the spinules on the shaft, typical radioles of *P. katherinae* resemble those of *Prionocidaris spinidentatus*; in the distinctly verticillate arrangement of the spinules of the radioles and in the apparently invariable presence of prominent, small nodules in addition to spinules on the shaft, this species is nearer *Prionocidaris cojimarensis*. A test from Palmer locality 1024 that may belong with the *P. katherinae* radioles from

that locality also is more similar to tests of *P. cojimarensis* than to those of *P. spinidentatus*.

Even if hybridization between cidaroid species were possible, and Mortensen (1928b) offered this as an explanation for several anomalies in Recent species, it is not likely that *P. katherinae* is a hybrid between *P. spinidentatus* and *P. cojimarensis*, for several reasons: the numerous known specimens of the latter two species are from localities distinct for each species; the localities from which *P. katherinae* specimens are known are different from all the localities from which the other two species have been collected; and the radioles of *P. katherinae* from the four different localities (three Cuban, one Puerto Rican) are more similar than would be expected in four random hybridizations. The distinctness of localities also indicates that *P. katherinae* is not simply a variant of either of the other two species.

The verticillate radioles of *P. katherinae* are much larger than those of the early Miocene species *Prionocidaris clevei* (Cotteau), discussed on following pages, yet have fewer spinules per whorl (14 to 16 in *clevei*). Also, tests of *P. clevei* differ from the one test here referred to *P. katherinae* in having much smaller areoles and wider median areas (see Table 9) and in having two inner tubercles on ambulacral plates, even in the smallest specimen.

The whorls of large, bladelike spinules on *P. katherinae* radioles resemble those on radioles of Recent Indo-Pacific *Prionocidaris verticillata* even more than on those of *P. cojimarensis*. Also, the horizontal ridge above the pores in the test fragment referred here to *P. katherinae* is so thick and the groove on the lower edge of the plate so narrow that the pores are considered subconjugate, more as in *P. verticillata*. However, the radioles are larger and spinules more projecting in *P. katherinae* than in the Recent species.

Like *P. cojimarensis*, *P. katherinae* bears considerable resemblance to early Miocene *Prionocidaris praeverticillata* from Kenya and Sind. Major differences are noted in Table 9. There may be genetic ties between these species, as discussed under "Evolution" in the "Synthesis" section.

The species is named for Dr. Katherine Van Winkle Palmer, Director Emeritus, Paleontological Research Institution, Ithaca, New York, whose help in many forms and encouragement were crucial to completion of this paper.

Table 9. — Selected characters of five *Prionoidaris* species: *P. cojimarensis* (early to late Miocene or Pliocene), *P. clevei* (early Miocene) and *P. katherinae* (early to middle Miocene or Pliocene) of the Caribbean area; the Tethyan species *P. praeverticillata* (early Miocene); and the Indo-Pacific species *P. verticillata* (Recent).

Characters	<i>P. cojimarensis</i>	<i>P. clevei</i>	<i>P. katherinae</i>	<i>P. praeverticillata</i>	<i>P. verticillata</i>
Radioles					
Max. length (mm)	25 ^e	19	34 ^a	31	38
Max. width (mm)	4.5	2.6	5.5	7	4
Max. no. of longitudinal series	35	16	25	29	20
No. whorls of large spinules	3-7	5	5 ^a	5-8	3-4
Max. projection of spinules (mm)	1.5	0.8	3.5	2.2	2
No. spinules per whorl	6-14	14-16	6-10	12-18	10-11
Nodule diameter (mm)	0.15-0.8	0.15-0.4	0.2-0.5	0.3-0.5	0.3-0.5
Max. collar length (mm)	2	1.2	2.5	1.5 ^b	0.6
Max. base length (mm)	1	0.7	2	2.5 ^b	1
Test					
Max. known HD (mm)	33 ^e	23 ^e	22 ^e	60 ^e	40
HD to which following apply (mm)	22 ^e	23 ^e	22 ^e	60 ^e	22
AmW/IAmW (%)	30	30	30	21 ^e	22-33
ArW/IAmPl W (%)	61	47	61	67	71-72
IAmPl:Col	7	7	7-8	?	5-6
AmPl:IAmPl	9	10	10	18	9-10
PorAW (mm)	0.7	1.3	1	1.5	0.8-0.9
IPorAW (mm)	1.8	2	1.4	3	1.5
IPorTub:AmPl	M+1	M+1-2	M+1-2	M+2-3	M+1

^e = estimate, ^a = known on broken radiole but estimated to be more, ^b = except 3.57 in a single specimen, ^c = except 2.38 in a single specimen (same as b above).

Holotype. — PRI 29661, a radiole fragment, now in two pieces (original one cut for cross section slide), collected by R. H. Palmer at Palmer locality 1024, lower cavernous limestones, Habana Province, Cuba.

Paratypes. — AMNH 18566/1,2; ANSP 50983; MCZ 4102; PRI 29635, 29720, 29746, 29749-29751.

Material. —

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radioles
NYAS/AMNH 117	AMNH 18566/1,2	C. A. Reeds	—	2
Palmer 813	?PRI 29747	R. H. Palmer	—	7 _a
Palmer 813	?PRI 29751	R. H. Palmer	—	2
Palmer 997	PRI 29749	P. J. Bermúdez	—	8
Palmer 997	PRI 29746	R. H. Palmer	—	16 _a
Palmer 997	PRI 29750	R. H. Palmer	—	1
Palmer 1024	ANSP 50983	R. H. Palmer	—	1
Palmer 1024	MCZ 4102	R. H. Palmer	1	—
Palmer 1024	PRI 29635	R. H. Palmer	—	20
Palmer 1024	PRI 29661 (holotype)	R. H. Palmer	—	1
Palmer 1024	PRI 29720	R. H. Palmer	—	3 _a

? = questionably referred to species, _a = includes ridged form of radioles.

Stratigraphic occurrence and localities. — middle Miocene (lower and upper cavernous limestones), Cuba; upper lower or middle Miocene possibly to Pliocene (Cibao limestone), Puerto Rico.

Measurements. — Test fragment: HD 22 mm; VD 10 mm; ApSD = PerD 11 mm (both estimated); IAmW 10 mm; AmW 3 mm (30% of IAmW); IAmPIW 5.6 mm; ArW 3.3 mm (61% of IAmPIW); MAW 1.6 mm (27% of IAmPIW); AdrAW 0.7 mm; PorAW 1 mm; IPorAW 1.4 mm.

Radioles: 34-?68 mm long, up to 5.5 mm wide; large spinules to 2.4 mm wide, projecting up to 3.5 mm; small nodules 0.2-0.5 mm in diameter, spaced 0.2-0.8 mm apart; minute (hair coat?) nodules 0.05-0.15 mm in diameter; collar up to 2.5 mm long, up to 0.2 mm wider proximally than distally; milled ring 0.1-0.3 mm wider than proximal end of collar; base up to 2 mm long, 1.2-1.5 times wider distally than proximally.

Prionocidaris clevei (Cotteau)

Plate 6, figures 7-12

1875. *Cidaris Clevei* Cotteau, p. 11, pl. 1, figs. 15-16.

1875. *Cidaris Anguillae* Cotteau, p. 11, pl. 1, figs. 17-18.

1876. *Cidaris Clevei* Cotteau, Cotteau, p. 126.

1876. *Cidaris Anguillae* Cotteau, Cotteau, p. 126.

1882. *Cidaris melitensis* Wright, Guppy [part], p. 194; 1921 reprint, p. 104.

1909. *Cidaris Clevei* Cotteau, Lambert and Thiery, 1909-1925, p. 145.

1909. *Cidaris Anguillae* Cotteau, Lambert and Thiery, 1909-1925, p. 145.

1922. *Cidaris clevei* Cotteau, Jackson, p. 20, pl. 1, fig. 11.

1922. *Cidaris anguillae* Cotteau, Jackson, p. 15, pl. 1, fig. 1.

1922. *Dorocidaris clevei* (Cotteau), Lambert, p. 594.

1922. *Cidaris anguillae* Cotteau, Lambert, p. 594.

Description. — Test small, commonly slightly flattened adorally, some specimens incurved at peristomial margin. Peristome, in only specimen where it could be measured (holotype), slightly smaller than apical system. Ambulacra nearly straight, wide. Ten ambulacral plates adjoining interambulacral plate at ambitus in largest known specimen, seven in smallest. Pores conjugate. Interporiferous area 1.5 to 2 times as wide as one poriferous area in plates at ambitus. Marginal tubercles in regular series; usually two smaller inner tubercles along lower edge of plate (in BM E18255, either one or two).

Seven to eight interambulacral plates per column previously recorded for holotype (smaller specimen), but further cleaning at oral margin of test revealed nine; seven present in two larger known specimens. Areoles slightly depressed, not quite half plate width. Areoles on adoral plates all separated by at least two double rows of scrobicular tubercles, those on plates at ambitus and above, by additional small tubercles. Primary tubercles moderately high; platforms smooth. Scrobicular tubercles round, only slightly larger than outlying tubercles. Median and adradial areas covered with small, crowded tubercles, these decreasing slightly in size to sutures. Median sutures slightly depressed, especially at corners of plates; narrow bare area along suture.

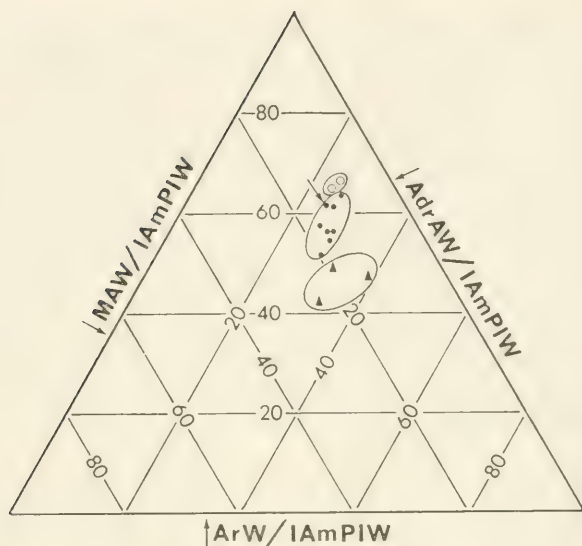
Radioles apparently not longer than horizontal diameter of test, slender, distally tapered. Only known tips slightly widened, rimmed with small, compressed spinules. Shafts having 14 to 16 longitudinal series of nodules. Interspersed among nodules along series on at least some radioles are compressed spinules arranged in five transverse whorls; each of proximal two whorls more or less double, oblique and with closely spaced spinules. No signs of hair coat noted on verticillate radioles. In several fragments (BM E18258-60) taken from same block as verticillate fragment (BM E18257), all ornamentation except few nodules near collar eroded away; indications of anastomosing hairs between nodules; whether specimens originally had whorls of spinules or were simply nodulose, as are some radioles of other *Prionocidaris* species, not now determinable. Col-

lars short, slightly narrowed proximally. Milled ring about same width as distal end of collar. Base short, slightly narrowed proximally. Acetabulum smooth.

Discussion. — The holotype of *Prionocidaris clevei*, with its exceptionally wide ambulacra and larger number of interambulacral plates per column stands apart from the other two tests here referred to the species. However, the range in ambulacral width/interambulacral width ratios (30 to 48 per cent) in these three specimens is not greater than the unusually wide range (22 to 40 per cent) in a measured series of Recent *Prionocidaris verticillata* of comparable size (see Appendix), and the three specimens agree well in other respects. It seems best then to consider them conspecific.

There is considerable resemblance between *P. clevei* and *Prionocidaris cojimarensis*, known from the Caribbean early to late Miocene. However, in *P. clevei*, the radioles are more tightly whorled, the areolar width is less and the median area width greater with respect to interambulacral plate width, and the inner tubercles on the ambulacral plates are more numerous than in *P. cojimarensis*. Although the tests of *P. clevei* are either about the same size as the smallest here referred to *P. cojimarensis* or smaller, it is unlikely that *P. clevei* was simply the young of *P. cojimarensis*. Not only is it not in the nature of cidaroids for the young of a species to have radioles with more specialized ornamentation (in this case, more tightly whorled spinules) than those of large specimens, but small radioles among the *P. cojimarensis* material that must have come from young specimens have whorls much less distinct than those in the small *P. clevei* radioles, as do also the large *P. cojimarensis* radioles. A study of series of specimens of Recent prionocidarids shows that the areole width/plate width ratio decreases and the median area width/plate width ratio increases with age, and if the number of ambulacral tubercles varies, it is the youngest specimens which have the fewest tubercles. In a triangular plot (Text-fig. 2), showing the interrelationships of plate, areole, median area, and adradial area widths, specimens of the above-mentioned two species of *Prionocidaris* fall into two groups, and the smallest of *P. cojimarensis* is well separated from the small *P. clevei* specimens. For these reasons, the two species are considered distinct.

P. clevei differs from *Prionocidaris katherinae*, another Caribbean Miocene species with verticillate radioles, in being an ap-



Text-figure 2. — Triangular diagram showing relationships of selected test characters (as percentages) for species of *Prionocidaris* (two) and *Tretocidaris* (one). Each point represents a single test specimen. Solid circles = *P. cojimarensis* (HD = 22-33 mm; arrow indicates 22 mm specimen); triangles = *P. clevei* (HD = 15-23 mm); open circles = *T. anguillensis* (HD = 16-24 mm).

parently smaller species, having smaller, more tightly whorled radioles with more spinules per whorl and smaller areoles, wider median areas, and a slightly greater number of inner ambulacral tubercles on the test (Table 10).

The radiole of *Cidaris anguillae* Cotteau (USNM 115393) here referred to *P. clevei* was collected by Dr. Cleve in Miocene deposits of Anguilla, as was the holotype of *P. clevei*. Although the *C. anguillae* radiole now has rounded nodules rather than spinules, this may be the result of erosion or over enthusiastic cleaning of the specimen; the nodules are longer than wide through the base, more like rounded off spinules than regular nodules, and they are arranged in oblique whorls. The radiole is near the size of those included in BM E18254-E18260.

Guppy (1882, p. 194) noted "in the matrix containing the specimen of *C. anguillae* is one broken example of the usual form figured

by Cotteau (1875, pl. 1, fig. 9, 10) as the spine of *C. melitensis*." For this reason, he placed *C. anguillae* (and *C. clevei*) in synonymy with *C. melitensis* Wright. The specimens figured by Cotteau are three radioles (USNM 115399) with shafts so eroded that they lack all surface ornamentation except a few nodules near the collar. These radioles were collected with two tests that here are referred to *Tretocidaris anguillensis* n. sp., and for that reason they were assigned to the same species. These three specimens are similar, in general configuration, to other radioles (BM E18258-E18260) found in the same matrix as a tightly verticillate radiole (BM E18257) and test fragments, all of which are here referred to *P. clevei*. It seems likely, therefore, that the radiole Guppy found in the same matrix as the *C. anguillae* radiole is a radiole of *P. clevei* like BM E18258-E18260.

That *T. anguillensis* has no relation to *P. clevei* is indicated by Text-figure 2; by a comparison of Table 10 and test data given under *T. anguillensis*, particularly with regard to the areole width/interambulacral plate width ratio and the number of ambulacral plates per interambulacral plate; and by the extensive bare areas along the median suture in *T. anguillensis*.

Possible origins of *P. clevei* and the other two Caribbean prionocidarids with verticillate radioles are discussed under "Paleobiogeography and Biostratigraphy."

Material. —

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Cleve (a)	USNM 115400 (holotype)	P. T. Cleve	1	—
Cleve (a)	USNM 115393	P. T. Cleve	—	1
Earle (a)	BM E18254-E18260	K. W. Earle	3	10

Stratigraphic occurrence and locality. — upper lower Miocene (Anguilla Formation), Anguilla.

Measurements. — For test measurements, see Table 10. Radioles (BM E18257-E18260): only known entire specimen, apparently not completely developed, 16 mm long, 1 mm wide. Three fragments from same matrix block match to form radiole 19 mm long, 2.6 mm wide, 2.4 mm thick; shaft with 14 to 16 series of nodules and interspersed large, compressed spinules in five whorls; large spinules 0.3-

Table 10. — Test measurements of *Prionocidaris clevei*.

Characters	BM E18256	BM E18255	USNM 115400 (holotype)
(in mm)			
HD	23.	20	15.
VD	12.5	12.5	9.5.
PerD	—	—	8.5
ApSD	—	—	9
IAmW	11.5	10	6.2
AmW	3.6	3	3
IAmPIW	6.2	5.3	3.6
ArW	2.9	2.6	1.5
MAW	2.4	1.7	1.2
AdrAW	0.9	1	0.9
PorAW	1.3	0.8	0.6
IPorAW	2	1.4	1.2
(as percentages)			
VD/HD	54.	62.5	59.
AmW/IAmW	31	30	48
ArW/IAmPIW	47	49	42
MAW/IAmPIW	39	32	33
(as numbers)			
IAmPl:Col	7	7	9
AmPl:IAmPl	10	10	7
IPorTub:AmPl	M+2	M+1-2	M+2

. = estimate.

0.6 mm wide, 0.7-1 mm long through base, projecting to about 0.8 mm; nodules 0.15-0.4 mm wide; collar 0.8-1.2 mm long, slightly less wide proximally than distally; milled ring about same width as distal edge of collar; base 0.6-0.7 mm long, decreasing from 1.5-1.6 mm distally to about 1-1.1 mm proximally.

One radiole (USNM 115393) with tip missing: 11 mm long, 3 mm at widest; shaft with 10 to 12 series of high, rounded nodules, about 0.5 mm wide; collar 1.5 mm long, nearly same width throughout; base 1 mm long, 1.8 mm wide distally, 1.2 mm proximally.

Prionocidaris cookei Cutress

Plate 9, figures 11-12

1976. *Prionocidaris cookei* Cutress, p. 191.

Description. — Original species description based on specimens collected in three localities of Chipola Formation, Florida, by Dr. C. Wythe Cooke (1394 radiole fragments plus 21 interambulacral plates; plates considered conspecific with radioles because they occur with them in two of three localities and resemble plates of Recent prionocidarid species).

Seven lots of radiole fragments from Cuba, comparable in most respects to the Florida material, are the basis for the following description. Fragments slender, tapered, slightly flattened, from radioles probably up to 35 mm long and 3 mm wide, having up to 16, commonly 12 to 14, series of uniformly small or small and medium-sized spinules. Dark banding apparent on several shaft fragments. Collars moderately long, either about same width throughout or widened toward milled ring. Milled ring well marked but not especially prominent. Bases up to 1.5 mm long, distinctly narrowed proximally. Acetabula smooth or, on some smaller radioles, crenulate along one side.

Discussion. — In a few of the Cuban radioles, which appear to be transitional from ambital to oral, the tips are slightly clubbed (wider than the shaft); such widening was not noticed in the Florida specimens. Spinules on the shaft project as much as 0.5 mm on the Cuban specimens, not more than 0.4 mm in the Florida specimens. There are no distinct nodules on the collars of the Cuban fragments, but this may be attributed to the small sample of basal fragments from Cuba. Otherwise, the Cuban radioles agree well with those from Florida. Test specimens that can be allied with the Cuban radioles are unknown.

Prionocidaris cookei differs from *Prionocidaris spinidentatus* in lacking massive, grossly spinulose radioles and from *Prionocidaris cojimarensis*, *Prionocidaris katherinae* and *Prionocidaris clevei* in not having the spinules of the radioles transversely aligned into whorls. *P. cookei* is nearer the Recent species *Prionocidaris hawaiiensis* (A. Agassiz and H. L. Clark) which occurs only in Hawaii. It differs from that species in having confluent tubercles on adoral plates, fewer ambulacral plates per interambulacral plate, shorter radioles, and adoral radioles that have the shaft longer than the collar.

Material. —

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez 83	PRI 29667	P. J. Bermúdez	—	30
Bermúdez 147	PRI 29668	P. J. Bermúdez	—	46
Palmer 378	PRI 29669	R. H. Palmer	—	4
Palmer 601	PRI 29670	P. J. Bermúdez	—	29
Palmer 601	PRI 29671	R. H. Palmer	—	18
Palmer 1034	PRI 29672	R. H. Palmer	—	23
USGS 2213	USNM 232505	C. W. Cooke	—	987

Material. — (continued)

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
USGS 2564	USNM 232503 (holotype)	C. W. Cooke	—	1
USGS 2564	USNM 232504	C. W. Cooke	19	32
USGS 3419	USNM 232506	C. W. Cooke	2	374

Stratigraphic occurrence and localities. — middle Miocene (Güines Formation; lower Yumurí Gorge series) and lower to upper Miocene or Pliocene (Cojimar Formation), Cuba; middle Miocene (Chipola Formation), Florida.

Measurements. — Caribbean radioles: maximum length estimated 35 mm; width 2-3 mm in most of largest specimens, to 3.5 mm in one transitional radiole; 10 to 16, but commonly 12 to 14, series of spinules; spinules 0.2-0.5 mm wide, projecting not more than 0.5 mm; collars 1.5-3.5 mm long; milled ring slightly wider than proximal end of collar; bases 1-1.5 mm long, 1.2-1.5 times wider distally than proximally.

See Cutress (1976, p. 192) for measurements of Florida specimens.

Prionocidaris loveni (Cotteau)

Plate 10, figures 1-19

1875. *Cidaris Loveni* Cotteau, p. 10, pl. 1, figs. 11-14.

1876. *Cidaris Loveni* Cotteau, Cotteau, p. 126.

1882. *Cidaris loveni* Cotteau, Guppy, p. 195; 1921 reprint, p. 105.

1887. *Eucidaris loveni* (Cotteau), Döderlein, p. 42.

1893. *Rhabdocidaris loveni* (Cotteau), Cotteau in d'Orbigny (1889-1894), p. 462.

1909. *Leiocidaris Loveni* (Cotteau), Lambert and Thiery, 1909-1925, p. 155.

1922. *Cidaris loveni* Cotteau, Jackson, p. 19, pl. 1, figs. 8-10.

1922. *Cidaris loveni* Cotteau, Vaughan, p. 111, 121.

1924. *Cidaris* sp. indet. Hawkins, p. 31.

1927. *Cidaris loveni* Cotteau, Arnold and Clark, p. 11, pl. 1, figs. 1-2.

1927. ?*Cidaris gymnozona* Arnold and Clark, p. 9, pl. 1, fig. 3.

1934. *Cidaris* aff. *loveni* Cotteau, Weisbord, p. 39, pl. 3, fig. 10.

1949. ?*Cidaris melitensis* Wright, Sánchez Roig, p. 26.

1961. *Phyllacanthus mortoni* (Conrad), Cooke, p. 4.

[probably not *Cidaris* cf. *loveni* Cotteau, Dickerson and Kew, 1917, p. 128; Israelsky, 1924, p. 138; *Cidaris loveni* Cotteau, Jackson, 1937, p. 229; all these reports based on one test fragment from the Miocene (Tuxpan Formation) of Mexico.]

Description. — In holotype (test from medium-sized cidaroid), apical system partly obscured but estimated about same diameter as peristome. Ambulacra slightly sinuate, one-third as wide as interambulacra. Eleven ambulacral plates per interambulacral plate at ambitus. Outer pores oval, inner, round; in few plates where determinable, pores separated by groove, this raised slightly on upper

part but pores nevertheless considered conjugate. Interporiferous area equal in width to one poriferous area. Marginal tubercles in regular series, bases contiguous. Inside marginals on each plate, one small tubercle at bottom edge of plate near median suture, in some specimens second one above it. Six or seven interambulacral plates per column. Areoles slightly depressed, a little more than half width of plate, all separated by double row of scrobicular tubercles except two in each column at adoral margin of test, these confluent. Tubercles all badly worn or broken but apparently moderately high and smooth originally. Scrobicular tubercles nearly round, separated by narrow ridge. Median and adradial areas otherwise covered with small tubercles, these decreasing in size up to sutures. Median suture slightly depressed.

In other test specimens thought conspecific with holotype, horizontal diameter up to 58.5 mm, apical system same (or nearly same) size as peristome, ambulacral width one-fourth to one-third interambulacral width, up to 19 ambulacral plates per interambulacral plate, interporiferous area of ambulacra either same width as or slightly narrower than one poriferous area in eight of ten specimens where this could be determined, 1.3 and 1.75 in other two, and up to three inner tubercles per ambulacral plate.

Interambulacra with up to eight, possibly nine, plates per column; areoles nearly half width of plates; scrobicular tubercles elliptical in best preserved specimens, separated by ridge or small tubercle; other secondary tubercles of slightly decreasing size up to sutures, arranged in longitudinal series in most specimens examined.

Radioles of three kinds. Apparently typical form slender to stout (up to 6.5 mm wide), slightly compressed, with 12 to 21 series of peaked nodules or coarse, low spinules, these staggered in adjacent series to give distinctive quincunx pattern. Only tips associated with this form (*e.g.*, in lot SUPTC 10246) not widened but with about six almost smooth ridges and indented end. Surface between and up sides of nodules and spinules covered with anastomosed hairs or sharply peaked nodules up to 0.08 mm in diameter, apparently remnants of coarse hairs. Collars of typical form no longer than 2.4 mm, commonly less, longer on one side because of oblique milled ring, and widened proximally. Base about same length as collar or slightly less, with one side longer than other and proximal width up to 1.3 times less than distal width. Acetabulum in basal

fragment in lot SUPTC 10245 apparently with faint crenulations along one edge; crenulations possibly present also in basal fragment in PRI 29743; other acetabula either distinctly smooth or too worn and chipped to determine presence or absence of crenulation.

Specimens of second form of radiole up to 8 mm wide. Shaft compressed, covered with small, closely spaced nodules having no evident regular arrangement; some having (in addition to nodules) large spinules projecting as much as 2 mm and slightly to distinctly compressed laterally. Seven such specimens with widely flaring tips pronged with pointed spinules; two of these (in PRI 29648 and PRI 29651) short (18 mm) but complete radioles, probably from adapical position on test. Best preserved of flared-tip radioles (PRI 29651) having collar 1.3 mm long and about same width throughout, shorter base, acetabulum too worn to distinguish crenulation (same true of all other fragments of this form with base intact). One lot (PRI 29679 from Palmer loc. 1090) includes radioles transitional between ambital and adoral types, these short, slightly flattened, with small nodules on shaft; tip not widened but ridged.

Five lots of fragments from smaller radioles apparently representing third form of radiole, differing from other two types in having peaked nodules or low spinules arranged in up to 12 straight, longitudinal series, these joined into ridges in some specimens. Shaft fragments up to 3.5 mm wide, slightly compressed. Along three to five of lateral and upper nodular series or ridges are a few larger, laterally compressed spinules, these projecting as much as 1.2 mm, either perpendicular to the surface or distally inclined and hooked. Large spinules more or less staggered in adjacent series. Surface between spinules and nodules covered with minute nodules (to 0.08 mm in diameter), probably either developing hairs or remnants of hairs. Collars up to 2.9 mm long, either uniform in width or slightly widened proximally. Bases shorter. Acetabula too worn to discern crenulations.

Discussion. — Previously, only a small test was known for *Prionocidaris loveni*. In collections made by Robert H. Palmer and Norman E. Weisbord, there are test and radiole fragments that can, with reasonable certainty, now be allied with the holotype of *P. loveni* even though some of Palmer's material is dated Oligocene and other specimens are Eocene.

Both Weisbord and Palmer collected test fragments (PRI 3806 and SUPTC 10245, respectively) from Loma Calisto, Nuevitas, Camagüey Province, Cuba (Weisbord loc. 2; Palmer loc. 1027) that in most characters, especially the unusually narrow interporiferous area, agree well with the holotype of *P. loveni*. These specimens and some radioles from the Loma Calisto site, in turn, agree well with radiole fragments and an interambulacral plate collected by Palmer at Palmer locality 1046. The radioles from these two Cuban localities are distinguished by the quincunx arrangement of the peaked nodules or low spinules on the shaft. Other test and radiole fragments that agree well with these specimens are included under "Material".

Referral of the nodulose, flared-tip radioles to *P. loveni* is based on the occurrence of this form in several lots of fragments with quincuncially arranged protuberances, and the presence of a fragment of this type in matrix still adherent to a *P. loveni* test fragment (ANSP 50986).

Specimens considered here to be from a third form of *P. loveni* radiole are considerably different from the other two, but the sparse, bladelike, large spinules recall those on the flared-tip *P. loveni* radioles, and two of the lots are from localities (Palmer locs. 1003, 1027) from which typical *P. loveni* radioles are known.

Extreme variability of this sort in radioles has been attributed here also to *Prionocidaris cojimarensis*, *Prionocidaris spinidentatus* and *Prionocidaris katherinae*. As mentioned in the discussion of *P. cojimarensis*, radiole variability is particularly notable in the Recent Indo-Pacific species *P. baculosa*. The three major forms of radioles in the latter species (nodules in quincunx pattern; nodules in quincunx pattern plus sparse spinules; nodules and spinules in distinct longitudinal series or ridges, lateral series particularly prominent) recall the three in *P. loveni* to such an extent that the possibility is suggested (under "Paleobiogeography and Biostratigraphy") that the two species may represent stages in a single evolutionary continuum or dual lineages from a common ancestor.

As regards the fossil prionocidarids with two or three forms of radioles, two assumptions can be suggested after consideration of Recent prionocidarids: (1) except for a few of the fossil radiole specimens, such as the short flared-tip radioles of *P. loveni* men-

tioned as having probably come from adapical plates or radioles that are obviously transitional (to oral), the fossil radioles can all be considered as having come from plates in the ambital region of the test; and (2) a variant form of fossil radiole came from an individual whose ambital radioles were all of that form; that is, the variants did not arise through loss of a typical form of radiole and regeneration to the variant form.

The *P. loveni* radioles with the quincunx pattern are similar to some of those from the lower Miocene of Kenya that Stephenson (1968, fig. 1e) referred to *Phyllacanthus opiparus* (Duncan and Sladen), a species known also from the Gáj series of Sind. They are even more like many of the Australian radioles of Oligocene and early Miocene age included by Chapman and Cudmore (1934, pl. 15, figs. 28-30) in their *Prionocidaris scoparia* and those illustrated by Philip (1963, pl. 21, figs. 5-7) as *Stylocidaris? scoparia* (Chapman and Cudmore). The test specimens of *P. loveni* are like those that Philip referred to *P. scoparia* and at least one of Stephenson's test fragments of *Phyllacanthus opiparus* (Stephenson, 1968, fig. 2j), especially in their narrow interporiferous areas. However, *P. loveni* apparently is not congeneric with either *Prionocidaris scoparia* or *Phyllacanthus opiparus*. In *P. scoparia*, the pores are nonconjugate, there is a high inner ridge on scrobicular tubercles like that in phyllacanthids, the primary tubercles all are smooth, and the tip of at least one radiole was flattened and slightly widened in a way not seen in known specimens of *P. loveni*. In transverse thin sections of the Kenyan *Phyllacanthus opiparus* radioles, Stephenson found distinct septal bundles such as are characteristic in phyllacanthids, whereas in a number of sections made from the *P. loveni* radioles, the septa run straight from core to cortex.

The interporiferous area in eight of the ten *P. loveni* test specimens is extraordinarily narrow; in cidaroids, this area usually is about twice as wide as one pore zone. However, a quick scan of Mortensen's monograph (1928b) bears out his observation (p. 11) that the relative width of the interporiferous area is of little classificatory value; he recorded narrow areas in five widely diverse genera and not in all species of those genera. Among those five genera, *Phyllacanthus* was the only one with conjugate or subconjugate pores, narrow areas being recorded for *P. imperialis*, *P. dubius* and *P. irregularis*. Apparently, even here it is not constant, for in 24 speci-

mens of *P. imperialis* and one of *P. dubius* measured during my study, the interporiferous area was distinctly wider in all but one (the largest, 72 mm, *P. imperialis*) and was slightly wider in that specimen. Although assignment to *Phyllacanthus* was seriously considered for specimens here assigned to *Prionocidaris loveni*, the lack of distinct inner ridges on the scrobicular tubercles of the test and septal bundles in radiole transverse sections as well as the presence of crenulations on some of the primary tubercles and the spinulose radioles associated with the tests with narrow interporiferous areas indicate that the species is better referred to *Prionocidaris*.

A specimen (BM E17207) collected by C. T. Trenchmann, apparently at the same time and place (Trenchmann loc. (a)) as *Cidaris* sp. indet. of Hawkins (1924, p. 312, 317), was examined during a visit to the British Museum (Natural History). Several interambulacral plates are embedded at various angles in the block of matrix. Only two are revealed to large extent. Ambulacral plates were not seen, but the interambulacral plate dimensions and the distinct linear arrangement of secondary tubercles on the median and adradial areas are much like those of the plates of *P. loveni*.

MCZ collections were searched carefully for the holotype and other specimens of *Cidaris gymnozona* Arnold and Clark (six or seven specimens were collected, apparently), but these were not found. The fact that the holotype of *C. gymnozona* is described as having an interporiferous area equal in width to one poriferous area suggests it may be referable to *P. loveni*. The holotype was collected by B. W. Arnold at a site (Arnold loc. (c)) suggested to him by Dr. Trenchmann and likely to be the same as or near Trenchmann locality (a) from which BM E17207 was collected, both localities being near Spring Mount, St. James, West Jamaica. One of Arnold and Clark's specimens of *P. loveni* was collected not far from Cambridge, St. James, lending further support to the possibility that *C. gymnozona* and *P. loveni* are conspecific. However, Arnold and Clark, while noting similarities between the two species, thought *C. gymnozona* was not referable to *P. loveni* because of its wide ambulacra, bare interporiferous area and difference in tuberculation of the plates. A bare interporiferous area is indeed different from that known in test specimens of *P. loveni*.

That the holotype of *C. gymnozona* may be, at least, a prionocidarid is indicated by pedicellariae which Hawkins found on the

specimen: "apparently small tridentate and small globiferous but not at all distinctive, resembling closely those of . . . *Eucidaris tribuloides*." The description would fit the pedicellariae of *Prionocidaris* perhaps even better than those of *Eucidaris*; in the latter, large globiferous pedicellariae are not uncommon (they are rare in *Prionocidaris*) and there are two kinds of small tridentate pedicellariae. If fossilized, tridentate pedicellariae of a prionocidarid (e.g., the Recent species *P. baculosa*) could easily be mistaken for those of *E. tribuloides* (see Mortensen, 1928b, pl. 87, fig. 1, pl. 86, fig. 16). Of course, the tridentate pedicellariae of *Tretocidaris* (Mortensen, 1928b, pl. 82, fig. 41) also resemble those of *E. tribuloides*, and the bare interporiferous area mentioned for *C. gymnozona* might suggest *Tretocidaris*. However, in that genus, large globiferous pedicellariae, not found with the holotype of *C. gymnozona*, are common and conspicuous.

A small test (USNM 232513) from the Eocene of Cuba (Finca "Santa Ana," Camagüey Province), must be mentioned in connection with *C. gymnozona*. It has conjugate pores and appears to be referable to *Prionocidaris*. The median area width is 31 per cent of the interambulacral plate width, wider than in specimens here referred to *P. loveni*, and it has tubercles that are more variable in size than in *P. loveni*. Although there appears to be a small inner tubercle on some of the ambulacral plates of this specimen, the interporiferous area appears bare, as mentioned for *C. gymnozona*. On the other hand, the interporiferous area is almost twice the width of a poriferous area. Tests of *P. loveni* may have been more variable than the specimens listed in the "Material" table suggest, or more than one species of *Prionocidaris* lived in the Caribbean area during the Eocene.

Jackson (1922, p. 20) considered *P. loveni* to be very similar to Recent *Tretocidaris bartletti* (A. Agassiz), "the only tangible difference being the more numerous tubercles and granules on the coronal plates." Measurements made during the present work indicate also that in *T. bartletti* the interporiferous area is usually twice as wide as one poriferous area and never as narrow as in *P. loveni*, and the pore area is not as sunken as in *P. loveni*. Also, radioles of the two species apparently are very different.

Sánchez Roig (1949, p. 27) recorded two radioles from "W. de Ciego de Avila, 42 km" (Palmer loc. 591); these he referred to

Cidaris melitensis, citing their similarity to some described by Jackson (1922, p. 21, pl. 1, fig. 15). The latter are three badly eroded specimens (USNM 115399) also figured by Cotteau (1875, pl. 1, figs. 9-10). They lack all surface ornamentation except a few nodules at the proximal ends of the shafts. A test collected by R. H. Palmer at Palmer locality 591 is referred here to *P. loveni*. Sánchez Roig's radioles may belong to the same species.

In two lots of *Prionocidaris spinidentatus* radiole fragments from Palmer locality 75 and Bermúdez locality (b), there are some fragments very much like some of the *P. loveni* radioles although other fragments in these lots are typical of *P. spinidentatus*. On the basis of radioles alone, these two species might be considered part of the same evolutionary sequence; however, the differences in widths of interporiferous and median areas in tests of the two species probably are too great to allow such a conclusion.

Material.—In addition to the listed specimens, a small test (USNM 232513) from "Eoceno, Finca 'Santa Ana,' Barrio Majagua, Jatibonico, Camagüey Province, Cuba," mentioned in the discussion, was examined. Sixteen specimens mentioned by Arnold and Clark (1927, p. 10), collected in Jamaica at Arnold localities (d) and (e), were not seen.

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Arnold (a)	MCZ 4159	B. W. Arnold	1	—
Arnold (f)	USNM 301378	B. W. Arnold	4	—
Bermúdez (a)	PRI 29648	P. J. Bermúdez	—	4 _b
Bermúdez 163	PRI 29649	P. J. Bermúdez	—	1 _c
Bermúdez 261	PRI 29650	P. J. Bermúdez	—	2 _c
Cleve (b)	USNM 115415 (holotype)	P. T. Cleve	1	—
Palmer 72	SUPTC 10244	R. H. Palmer	—	1
Palmer 165	PRI 29759	R. H. Palmer	—	1
Palmer 165	PRI 29651	P. J. Bermúdez	—	3 _a
Palmer D103	ANSP 50986	R. H. Palmer	1	—
Palmer 491	PRI 29652	R. H. Palmer	—	5
Palmer 591	ANSP 50987	R. H. Palmer	1	—
Palmer 1003	LSJU 53245	R. H. Palmer	—	5
Palmer 1003	SUPTC 10257	R. H. Palmer	—	3 _c
Palmer 1027	PRI 29743	R. H. Palmer	—	6
Palmer 1027	SUPTC 10245	R. H. Palmer	—	10
Palmer 1027	SUPTC 10258	R. H. Palmer	—	1
Palmer 1046	ANSP 50979	R. H. Palmer	1	—
Palmer 1046	PRI 29740	R. H. Palmer	—	7 _b
Palmer 1046	PRI 29744	R. H. Palmer	—	21
Palmer 1082	CASGTC 58722	R. H. Palmer	—	3 _c
Palmer 1090	PRI 29679	R. H. Palmer	—	15 _c
Palmer 1090	PRI 29742	R. H. Palmer	—	1

Material. — (continued)

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Palmer 1627	PRI 29741	R. H. Palmer	—	5
Palmer 1640	SUPTC 10246	R. H. Palmer	—	3
Trenchmann (a)	BM E17207	C. T. Trenchmann	1	—
Weisbord 2	PRI 3806	N. E. Weisbord	1	—

a = radiole fragments having finely nodulose shafts and widely flared tips, b = radiole fragments having both nodulose shafts and flared tips, and quincunx-patterned nodule series, c = radioles having straight series of nodules and compressed spinules. Specimens in other lots all have nodules in quincunx pattern.

Stratigraphic occurrence and localities. — upper Eocene (St. Bartholomew limestone), St. Bartholomew; middle Eocene (Loma Candela Formation), upper Eocene (Jabacoa Formation) and Oligocene, Cuba; middle Eocene (yellow limestone), Jamaica.

Measurements. — For test measurements, see Table 11. Radiole fragments with quincunx pattern: probably from radioles up to 50 mm long; known specimens 2.3×2.5 to 5.5×6.5 mm wide; peaked nodules or low spinules 0.2-0.9 mm in diameter; minute (hair coat?) granules 0.12-0.18 mm in diameter; collar 1-2.4 mm long, 0.2-0.6 mm shorter on one side than other, and 0-0.7 mm wider proximally than distally; milled ring usually 0.1-0.2 mm, but up to 0.5 mm, wider than proximal end of collar; base 1-2.6 mm long, 0.2-0.5 mm longer on one side than other, and 0.7-2 mm narrower proximally than distally.

Fragments from nodulose-shafted radioles with flared tips: 5-8 mm wide, up to 2 mm less in aboral-adoral axis; flared tips 8×7 to 15×12 mm wide, including sharp spinules 5 mm long; small nodules 0.2-0.4 mm in diameter; large spinules to 3.5 mm long and 2.5 mm wide through base and projecting up to 2 mm; minute (hair?) granules up to 0.08 mm in diameter; the few intact collars up to 1.5 mm long and scarcely widened proximally; milled rings and bases too eroded to measure. Two adapical (?) radioles of this form both 18 mm long, with tips up to 10 mm wide; nodules and spinules as above; collars in best specimen 1.5 mm long, 3 mm wide throughout; milled ring 3.2 mm wide; base 0.8 mm long, 2.7 mm wide distally, 2.1 mm proximally.

Fragments from radioles having straight series of nodules and spinules (questionably referred to *P. loveni*): largest shaft fragments 2.7×2.6 to 3.5×3.4 mm wide; nodules and low spinules 0.2-0.5 mm wide; largest spinules 1.8 mm long and 0.8 mm wide through

Table 11. — Measurements of test specimens of *Prionocidaris loveni*.

Characters	USNM 301378	USNM 301378	ANSP 50974	ANSP 50987	ANSP 50986	USNM 301378	PRI 3806	MCZ 3261 _b	MCZ 4159	USNM 115415 _a	SUPTC 10245
(in mm)											
HD	58.5	50 _e	—	43 _e	43 _e	40.5 _e	40 _e	35	32	28	—
VD	50	46	—	—	24	31	—	20	18 _e	15	—
PerD	20 _e	20 _e	—	—	—	14 _e	—	11.5 _e	12	11	—
ApSD	20	19 _e	—	—	—	15	—	12.5 _e	13	11 _e	—
IAmW	29	27	—	18 _e	18	20	17 _e	14	15	12	—
AmW	7.5	6	—	5	5	6	3.6	4	5	3.9	1.4
IAmPIW	16	15	14.5	10	10	11	8.2	8	9	7	4
ArW	9.5	9	10	7.2	6	5	5.5	4.5	5	4	2.5
MAW	4	3.5	3.5	1.8	2.5	3	2	1.5	2.5	1.8	1
AdrAW	2.5	2.5	1.5	1	1.5	1.5	0.7	1	1.5	1.3	0.5
PorAW	2	2	—	1.7	1.5	1.5	1.2	1.5	1.7	1.3	0.7
IPorAW	3.5	2	—	1.6	2	2	1.2	†	1.5	1.3	0.7
(as percentages)											
VD/HD	85	92	—	—	58	76 _e	—	57	75	54	—
AmW/IAmW	27	22	—	28	28	30	21 _e	29	33	32.5	—
ArW/IAmPIW	59	60	69	72 _e	60	45	67	56	56	57	63
MAW/IAmPIW	25	23	21	18	25	27	24	19	28	25	25
(as numbers)											
IAmPl:Col	8	8	—	—	7-8	7-8	—	7	8	6-7	—
AmPl:IAmPl	19	16	14	16	13	15	16	13	13	11	9
IPorTub:AmPl	M+2	M+2	—	M+1	M+1-3	M+1	M+1	M+1	M+1-2	M+1	M+0

^a = holotype of *P. loveni*, _b = holotype of *Cidaris gymnozona*, _c = estimate, ? = measurable but not given by Arnold and Clark, † = not measured, but equal.

base and projecting up to 2 mm; minute granules up to 0.08 mm in diameter. One basal fragment with collar 1.5 mm long, 2 mm wide distally, 1.9 mm wide proximally; milled ring worn to same width as proximal collar; base about 1.3 mm long, 1.7 mm wide distally, 1.2 mm wide proximally.

Genus **FELLIUS**, new genus

Type-species. — *Cidaris foveata* Jackson, 1922, p. 17, pl. 1, figs. 6-7, the only species now known.

Diagnosis. — Test low in profile; with widely separated, conjugate pores and high, prominent, deeply crenulate tubercles; median interambulacral suture in some specimens deeply depressed into pits at corners of plates. Primary radioles distinctly flattened and laterally serrate; having smooth or sparsely spinulose longitudinal ridges, minute nodules, and, in large specimens, irregular fine ridges on adapical and adoral surfaces.

Discussion. — *Fellius* is closest to *Porocidaris* Desor. Both have flattened, laterally serrate radioles and medium-sized tests with low profile, conjugate pores, and high and deeply crenulate tubercles. *Fellius* differs from *Porocidaris* in lacking groovelike pores in the areoles, in having (in some, but not all, specimens) deep depressions at the median angles of the interambulacral plates; and in having all but the lowest two primary areoles separated by at least a single row of scrobicular tubercles.

The generic name is masculine. It honors Dr. H. Barraclough Fell, Museum of Comparative Zoology, Harvard University, who at the time I borrowed the holotype of *Cidaris foveata* for study recognized that it probably represented a new genus.

Stratigraphic occurrence and localities. — Eocene of Jamaica and Cuba.

Fellius foveatus (Jackson)

Plate 11, figures 1-9

1922. *Cidaris foveata* Jackson, p. 17, pl. 1, figs. 6-7.

1922. *Cidaris foveata* Jackson, Vaughan, p. 111.

1949. ?*Cidaris foveata* Jackson, Sánchez Roig, p. 26.

1953. *Porocidaris lopezi* Sánchez Roig, p. 137, pl. 1, fig. 4.

Description. — Test moderately large and having a slightly depressed adapical edge and flat adoral surface. Apical system slightly larger than peristome. Ambulacra nearly straight and a little more than one-third as wide as interambulacra. Eleven ambulacral plates

per interambulacral plate at ambitus in largest (HD 52.5 mm) specimen. Poriferous areas slightly depressed. Pores oval, about equal in size, widely spaced and conjugate. Wall between pores low, creased by shallow horizontal groove in well-preserved plates. Horizontal ridge along upper edge of each plate high and narrow. Interporiferous area about twice width of one poriferous area; median suture distinctly depressed. Marginal tubercles in regular series. Slightly smaller tubercle inside marginal on each plate, this tubercle usually situated on upper part of plate and more than half of plate height and one to three, usually two, small tubercles along lower part of plate.

Nine to 10 interambulacral plates per column in largest specimen. Areoles large, all separated by scrobicular tubercles except on two adoral plates per column. Tubercles large and high, rising steeply from scrobicule. Eleven to 12 deep crenulations scoring entire circumference of platform. Mamelon perforate. Scrobicular tubercles nearly round, well separated. Ring of smaller tubercles outside scrobicular ring. Median and adradial areas otherwise covered with small tubercles of decreasing size extending to sutures; these tubercles on large specimens separated by horizontal grooves. Median interambulacral suture depressed slightly to deeply, particularly at corners of plates where there may be distinct pits.

Radioles of two kinds; slimmest probably from small specimens or new radioles on older specimens. Both kinds flattened, laterally serrate, and apparently only slightly tapered distally. Tips unknown. In addition to lateral series of serrations, shaft having five to six ridges on upper surface and three to five on adoral surface. In slender radioles, lateral serrations low but long through base. Other ridges low and smooth or slightly undulate. Surface of these slender radioles otherwise covered with minute nodules. In larger radioles, lateral serrations coarse, projecting as much as 1 mm. Median ridge bearing prominent spinules; two or more other ridges on some specimens bearing small spinules. Ridges otherwise smooth or undulate. Surface between ridges on upper surface of radioles ornamented with fine ridges or irregular series of granules and other irregularities of uneven size and arrangement, giving "sculptured" appearance. Minute nodules, possibly remnants of hairs, covering protuberances and surface between them. Collars up to 6 mm long and slightly to moderately widened proximally; faint indications on one of frag-

ments that collars were nodulose. Milled ring worn on most specimens but appearing not to have been especially prominent. *Acetabulum* deeply crenulate.

Discussion.—The holotype is the only specimen known at present with deep interambulacral pits. Two of the other three Jamaican test specimens show only slight depressions in the median suture, the other almost none. However, their large, high, deeply crenulate tubercles and widely spaced, conjugate pores clearly indicate that these tests are conspecific with the holotype.

Although some of the pits in the holotype are filled with foreign matter and some have obviously been gouged by some force, others are clear of sediment and undamaged. The latter can be seen to be true pits, the small tubercles of the median area continuing into them to the sutures. The pits in *Fellius* are very different from those in *Goniocidaris* and *Stereocidaris*. The latter are bare areas extending for a variable distance along the horizontal and(or) median suture. In *Fellius*, an incurving of the corners of the plates, not a lack of ornamentation, produces the depressions.

Several radiole fragments were found in the matrix adhering to one of the Jamaican test fragments (MCZ 4158A). The largest of these recalls the Cuban radiole fragments from Palmer locality 1064; the others are more like those from Palmer's Cuban locality 687. They provide evidence that the large, "sculptured" radioles, the smaller, ridged radioles, and the tests all belong to the same species.

The two radiole fragments (LSJU 53246) from Palmer locality 1027 are so badly eroded that few surface features remain. Because the shafts are so distinctly flattened, they are referred to the species, although questionably.

Cidaris foveata was recorded by Sánchez Roig (1949, p. 26) from two localities in Cuba, but numbers or kinds of specimens were not specified nor were a description or illustrations provided, so the record is questionable.

Fellius foveatus is very close to *Porocidaris anomala* Duncan and Sladen (1882-1886, p. 113, pl. 21, figs. 10-14) from the upper Eocene (Nummulitic strata, Khirthar series) of western Sind (Pakistan) and resembles also *Rhabdocidaris zitteli* Lorient (1863, p. 8, pl. 1, figs. 1-1d, 11-11b) described from the Nummulitic of Egypt and reported from the lower Eocene (Danman Formation) of Qatar in the Persian Gulf area (Roman, 1976, p. 51, pl. 3, fig. 1, text-fig.

1) and, to less extent, resembles *Rhabdocidaris* sp. cf. *R. zitteli* Loriol recorded from the lower Eocene (Upper Auradu series) of British Somaliland (Kier, 1957, p. 84, pl. 103, figs. 1-2). There may be genetic ties, at least on a generic level, between *P. anomala* and *R. zitteli*. The test of *F. foveatus* resembles that of the other two species in its low profile, nearly straight, wide ambulacra, and protruding, deeply crenulate tubercles. All three species have flattened radioles with serrate edges.

The main difference between the tests of *F. foveatus* and *P. anomala* are lack of even faint areolar depressions in *F. foveatus*, the apparent lack of any interambulacral depressions in *P. anomala*, confluence of areoles in *P. anomala* but not in *F. foveatus*, a greater number of interambulacral plates per column in *P. anomala* (12 or 13 in the 48 mm HD *P. anomala* test, 9 to 10 in the 52 mm HD *F. foveatus* test), and fewer ambulacral plates adjoining an interambulacral plate at the ambitus in *P. anomala* (8 in the 48 mm HD *P. anomala* test, 9 and 11 in the *F. foveatus* tests of 40 mm and 52 mm HD, respectively).

Duncan and Sladen had two tests but only one radiole of *P. anomala*. The radiole appears from their illustration and description (1882-1886, p. 114, pl. 21, fig. 4) to be similar to the slender radioles of *F. foveatus*. A number of interambulacral plates and radiole fragments, previously unrecorded, that are referable to *P. anomala* were taken in well drillings in Eocene strata in Libya by Esso Standard, Inc. and made available for this study. These have been deposited in three museums and now bear catalogue numbers USNM 167237, MCZ 4160, 4161, and BM E75730-E75741. The Libyan *P. anomala* radioles show similarities to the *F. foveatus* radioles, particularly the slender ones. However, they are a little smaller and have slightly coarser lateral serrations.

The Libyan plates also agree well with those of *P. anomala* except that none of them shows any sign of areolar depressions. However, Duncan and Sladen (1882-1886, p. 114) indicated that in *P. anomala* the "characteristic is very feebly marked throughout, and where weathering influences have taken place is altogether undiscernible." The Libyan plates are weathered. It appears likely they, as well as the radioles, are referable to *P. anomala*.

On a species level, there are enough differences to separate *P. anomala* and *F. foveatus*. However, because the areolar depressions

in *P. anomala* are not deeply incised as in *Porocidaris schmidelii* Münster (type-species of *Porocidaris*) and may be absent altogether, and because interambulacral depressions are not a constant feature in *Fellius*, it may be that *P. anomala* could be referred to *Fellius*.

Stefanini (1924, p. 833) mentioned that the West Indian species *Rhabdocidaris foveata* and the European Eocene species *Rhabdocidaris pouechi* Cotteau were related. A nearly perfect test of the latter species figured by Cotteau (1887, p. 636, pl. 10, figs. 7-9) does appear similar to *F. foveatus* as well as *P. anomala* and *R. zitteli*. In illustrations, Cotteau's specimen probably is nearer the specimen identified by Kier (1957, p. 84) as *Rhabdocidaris* sp. cf. *R. zitteli* Loriol in having primary tubercles centered on the plate and narrower ambulacra (near 30 per cent of the interambulacral width) than those in *F. foveatus* (34 to 38 per cent) or *P. anomala* (40 per cent).

Material. —

Locality	Catalogue Number	Collector	Number of specimens Test	Radiole
Arnold (a)	MCZ 3234 (holotype)	B. W. Arnold	1	—
Arnold (b)	MCZ 4158a-c	B. W. Arnold	3	6
Oberlin (a)	PRI 29752	Unknown	2	1
Palmer 687	SUPTC 10005	R. H. Palmer	—	4
Palmer 1027	LSJU 53246	R. H. Palmer	—	2
Palmer 1064	SUPTC 10004	R. H. Palmer	—	3

Stratigraphic occurrence and localities. — Eocene of Cuba and Jamaica; levels not specified on labels or in locality lists. The Jamaican localities were not detailed, but the type-locality comprised yellow limestone, probably the Cambridge Formation of R. T. Hill.

Measurements. — For test measurements, see Table 12. Radioles: largest fragments, 4.3-5 mm wide and 3.2-4.2 mm thick at the widest portion of shaft; largest spinules 0.8-1.1 mm wide and 0.8-2.4 mm long through base on lateral and adapical surfaces of shaft, slightly less on adoral surface, and projecting up to 1 mm; smaller spinules 0.2-0.5 mm in diameter; fine ridges and nodules 0.12-0.3 mm wide; minute granules (remnants of hairs?) up to 0.08 mm in diameter; collars 3.2-6 mm long; bases 1.3-1.6 mm long.

Genus **PROPHYLLACANTHUS**, new genus

Type-species. — *Leiocidaris leoni* Lambert and Sánchez Roig

Table 12.—Measurements of known test specimens of *Fellius foveatus*.

Characters	MCZ 3234 (holotype)	MCZ 4158a	MCZ 4158c	MCZ 4158b
(in mm)				
HD	52.5	—	40.	33.
VD	33.5	—	25.	19.5
PerD	16.5.	—	14.	12.
ApSD	18.5.	—	15.5.	14.
IAmW	22.5	22	18	14.5
AmW	8	7.5.	7	5.5
IAmPIW	13	12	10	8
ArW	7.5	8	6	5
MAW	3	3	2.5	2
AdrAW	2.5	2	1.5	1
PorAW	2	2	2	1.5
IPorAW	4	4	3	2.5
(as percentages)				
VD/HD	64	—	64.	61.
AmW/IAmW	36	34.	39	38
ArW/IAmPIW	58	67	60	62.5
MAW/IAmPIW	23	25	25	25
(as numbers)				
IAmPl:Col	9-10	8-9	8-9	8-9
AmPl:IAmPl	11	10	9	8
IPorTub:AmPl	M+3-4	M+2-3	M+1-3	M+1-2

. = estimate.

in Sánchez Roig (1926, p. 33, pl. 4, figs. 5-6), from the Cretaceous of Cuba and Jamaica.

Diagnosis.—Test having conjugate pores and moderately high tubercles, some of latter finely crenulate around entire platform or along its upper edge. Radioles slender to moderately robust, cylindrical; having numerous, more or less regular, longitudinal series of small, sharp, finely serrate (in some specimens) nodules or nodular ridges and showing evidence of hair coat. Septa of shaft arising in bundles in some radioles.

Discussion.—The genus *Prophyllacanthus* may be the evolutionary link between *Phyllacanthus* and *Rhabdocidaris*. In its conjugate pores, large primary areoles, and closely tuberculated median and adradial areas of interambulacral plates, it resembles both of those genera. Some of its upper tubercles are weakly crenulate; deep crenulations of all or most primary tubercles are characteristic of *Rhabdocidaris*, but in *Phyllacanthus* all tubercles are entirely smooth. *Prophyllacanthus* radioles, having septal bundles and finely nodulose ridges or series of small nodules, are more like those of

Phyllacanthus. No record was found of bundles in rhabdocidarid radioles, and these radioles are commonly more or less spinulose and apparently larger and stouter.

As mentioned in the discussion of *Prophyllacanthus leoni*, the same or closely related species may have occurred in the Indian region during the Cretaceous. If this can be demonstrated, it would indicate that *Prophyllacanthus* may have spread throughout Tethys during that period.

Because it appears likely that the new genus is the forerunner of *Phyllacanthus*, the name *Prophyllacanthus* is appropriate. The name is masculine.

Stratigraphic occurrence and locality. — Upper Cretaceous (including Habana Formation, Big Boulder Bed Member), Cuba; Upper Cretaceous (Maestrichtian), Jamaica.

***Prophyllacanthus leoni* (Lambert and
Sánchez Roig in Sánchez Roig)**

Plate 12, figures 5-11

1923. ?*Leiocidaris* sp. indet. Hawkins, p. 205.

1926. *Leiocidaris Leoni* Lambert and Sánchez Roig in Sánchez Roig, p. 33, pl. 4, figs. 5-6.

1927. ?*Leiocidaris* sp. Hawkins, Arnold and Clark, p. 12.

1931a. *Dorocidaris Molinetti* Lambert, p. 299, text-fig. 3, pl. 17, figs. 14-15.

1949. *Phyllacanthus Leoni* (Lambert and Sánchez Roig), Sánchez Roig, p. 27.

1949. *Dorocidaris molinetti* Lambert, Sánchez Roig, p. 28.

1949. *Dorocidaris demujiensis* Sánchez Roig, p. 30.

1949. *Dorocidaris damujiensis* [*sic*] Sánchez Roig, pl. 1, fig. 1.

1949. *Dorocidaris madrugensis* Sánchez Roig, p. 32. [Not *Dorocidaris madrugensis* Sánchez Roig, 1949, pl. 1, fig. 2]

1949. *Leiocidaris madrugensis* Sánchez Roig, pl. 1, fig. 2. [Not *Leiocidaris madrugensis* Sánchez Roig, pl. 1, fig. 4]

1952. ?*Dorocidaris garciai* Sánchez Roig, p. 2, pl. 1, fig. 3.

Description. — Test large, high. Apical system smaller than peristome. Ambulacra wide, slightly sinuate. Nineteen to 21 ambulacral plates per interambulacral plate at ambitus in largest specimen (HD 67 mm). Pores widely spaced and distinctly conjugate in few well-preserved areas of known tests although wall between pores in most areas worn smooth, erasing depression on lower edge of each plate. Interporiferous area about 1.5 to 1.6 times as wide as one pore area; median suture not depressed. Marginal tubercles mamelonate, those on adjoining plates forming regular series. Inside marginals, one or two smaller tubercles per plate; at ambitus in largest specimen, possibly an additional two or three smaller tubercles.

Eight to nine interambulacral plates per column in largest specimen examined. Tubercles large, perforate, either all smooth or those on upper part of test crenulate, in some specimens around entire circumference but usually just along upper edge of platform. Areoles circular on upper part of test, elliptical adorally. Scrobicular tubercles distinctly elliptical in well-preserved specimens and separated by ridge; inner edge raised and sharply cut, as in phyllacanthids. Outside scrobicular ring, smaller tubercles crowded on plate to sutures. Edges of plates distinctly incurved. Median area narrow. On one interambulacral plate (SUPTC 10248; Palmer loc. 1120), scrobicule of tubercles marked by very faint swirl pattern, this extending inward 0.4 to 0.5 mm from outer edge.

Largest of known radiole fragments were from robust, cylindrical radioles estimated to have been 60 or more mm long and up to 5 mm wide. Shaft having up to 50 more or less regular series of small, sharply peaked, finely serrate (in some specimens) nodules or nodulose ridges that are smallest and most closely spaced on adoral surface of radiole. Surface between and up sides of nodules and ridges covered by minute granules, possibly remnants of hair coat. Neck 0.5 to 1 mm long visible on some specimens. Collars on most specimens moderately long, distinctly widened toward milled ring, and, on best-preserved specimens, scored distinctively throughout entire length by longitudinal ridges and deep grooves, these particularly prominent proximally. Distal portion of collar in several specimens having ridges giving way to series of fine granules about 0.027 mm in diameter. Milled ring well marked but not projecting, sometimes oblique; grooves of ring on some radioles extending part way down base. Base narrowed proximally to 70 to 80 per cent of distal width; acetabulum smooth or crenulate either around entire circumference or along only one edge. Septa of middle layer of shaft arising in bundles, visible in transverse sections, as in phyllacanthid radioles.

Discussion.—In slender radioles, apparently from juveniles, there may be discrete, closely spaced nodules, as described above, near the collar but distally there are nearly straight, crenate ridges spaced up to 0.3 mm apart. Alone such distal fragments could easily be mistakenly referred to species of *Stereocidaris* or *Cidaris*. As the slender radioles increase in size during growth of the echinoid, ad-

ditional series apparently form on the proximal shaft and gradually extend distally. The number of series increases disproportionately to the increase in diameter of the radiole, so the spacing between the series becomes narrower.

In one fragment (PRI 29757; Bermúdez loc. (d)), the collar is unusually long (9 mm), and the ridges of the shaft are narrower and more closely spaced than in typical *P. leoni* radioles, that is, those from Jamaica and from Cuban Palmer locality 1120. However, this fragment is definitely phyllacanthid (septa arise in bundles). A few of the fragments from Cuba (Palmer loc. 2191) also have long collars. The specimens are grouped here with *P. leoni* but may belong to a third *Prophyllacanthus* species.

Palmer's Cuban specimens include two remarkably well preserved tests. There are both crenulate (on the upper part of the tests) and smooth tubercles on the specimens. A small test collected in Jamaica by U.S. Geological Survey scientists also has both crenulate and smooth tubercles. In a few well-preserved fragments (also collected in Jamaica by the USGS) from what must have been a test as large as Palmer's largest, the tubercles all are smooth, even on upper plates, but in all other respects these specimens are similar to the Cuban tests. Radiole fragments collected with the Jamaican fragments are like the Cuban *P. leoni* radioles from Palmer locality 1120 (SUPTC 10248) except that all acetabula are smooth.

Although the two tests that are the basis for *Leiocidaris leoni* Lambert and Sánchez Roig in Sánchez Roig were described as having smooth tubercles, crenulations, if they had been present, were probably obscured during fossilization. According to Sánchez Roig (1949, p. 27), the smaller test (HD 55 mm) was so badly preserved that the mamelons were eroded on almost all the plates, and the larger test (HD 63 mm) had been ruined by acid.

Dorocidaris molineti Lambert was based on a test (HD 48 mm) that was described as having crenulate tubercles and widespread pores but was placed in *Dorocidaris* because the pores were separated by an elongate swelling. As illustrated, this wall is much wider than is usual in species with nonconjugate pores. In some of the Cuban specimens here referred to *Prophyllacanthus leoni*, there are areas of the ambulacra in which the wall between the pores is worn smooth so that all indications of conjugate pores are lost, but in better preserved areas, the lower part of the wall is distinctly depressed. Wear

probably had obscured the conjugate nature of the pores in the test of *D. molineti*. Because in other respects the description of the test of *D. molineti* fits *P. leoni* well, *D. molineti* is here considered a synonym of *P. leoni*.

Two interambulacral plates and one radiole fragment were the basis for *Dorocidaris demujiensis* Sánchez Roig (1949, p. 30, pl. 1, fig. 1). The plates were described as differing from those of *D. molineti* only in being somewhat lower and having thinner edges. The illustrated radiole fragment appears to be like those known for *P. leoni*; *D. demujiensis*, therefore, also is placed in synonymy with *P. leoni*. Sánchez Roig (1949, p. 32) described another species, *Leiocidaris madrugensis*, which also belongs to *P. leoni*. The interambulacral plate and radiole fragment illustrated in his pl. 1, fig. 2 are much like those of *P. leoni*.

Dorocidaris garciai Sánchez Roig (1952, p. 2, pl. 1, fig. 3) also may belong in *P. leoni*. The species is based on a weathered test; the illustration shows that the test has widely spaced and conjugate pores and in other respects resembles tests of *P. leoni*. However, it has a narrower interporiferous area (IPorAW = PorAW) and slightly narrower median areas.

Hawkins (1923, p. 205) mentioned as *Leiocidaris* sp. a single interambulacral plate and an adjoining half ambulacrum that had been collected from Cretaceous strata in Jamaica. He mentioned some similarity of the specimen to *Leiocidaris hemigranosus* (Shumard). This may be *P. leoni*, but there was no illustration and I did not locate the specimen. Arnold and Clark (1927, p. 12) mentioned the same specimen in connection with *Cidaris loveni* but also noted that Hawkins considered the relationship to be doubtful. The fact that *Prionocidaris loveni* is Eocene and the specimen in question is Cretaceous may indicate that they are not the same.

Prophyllacanthus leoni probably was the ancestor of the Caribbean Eocene phyllacanthid here described as new.

From Middle Albian strata of Maruim, Sergipe, Brazil, Maury (1936, p. 263, pl. 2, figs. 4-5) described as *Rhabdocidaris brasiliensis* a test fragment from a large cidaroid with conjugate pores and tubercles that may have been crenulate. A radiole that probably belonged with the fragment was described as "ornamented with narrow, closely-set, sharply defined, parallel, longitudinal ridges which are beset with thorny tubercles"; it was 5 mm wide. The description

strongly suggests that this species belongs to *Prophyllacanthus*. That it probably is not the same as *P. leoni*, however, is indicated by its greater age and the fact that Maury believed it to have few (probably not more than six) interambulacral plates per column. Large tests of *P. leoni* have eight to nine such plates per column.

There are striking similarities between the specimens here referred to *P. leoni* and some of the specimens which Duncan and Sladen (1882-1886) described and illustrated from the Ranikot series (Paleocene) of Sind: *Phyllacanthus sindensis*, a test fragment consisting of four interambulacral plates and a few adjoining ambulacral plates (p. 27, pl. 5, figs. 11-12); *Phyllacanthus* sp., part of an interambulacrum with adjoining ambulacral plates (p. 28, pl. 5, figs. 4-5); and "spines of a species of *Cidaris*" (p. 50, pl. 10, figs. 9-14). All were collected in the same locality and probably at the same time (all bear the same "survey-number": G280/135). Two of the radioles (basal fragments) have shafts with closely set nodules ("small, close, bluntly serrate knobs"); the acetabulum is smooth on one, crenulate on the other. The test fragment of *P. sindensis* has wide ambulacra and conjugate pores. The interporiferous area of each ambulacral plate bears a marginal tubercle and one inner tubercle (about equal in size to the marginal) and a minute tubercle. Tubercles on the interambulacral plates are crenulate. The *P.* sp. test fragment appears similar to that of *P. sindensis* but has, in addition, "very indistinct remains of furrows close to the scrobicular circle, converging towards the base of the boss," recalling the swirl pattern of the Cuban interambulacral plate (SUPTC 10248; Palmer loc. 1120) mentioned above. Because the Pakistani specimens were not examined during this study, I can not assert that the Caribbean and Pakistani specimens are conspecific, but they seem closely related.

There apparently was at least one species with similarities to phyllacanthids in Texas during the Cretaceous. *Stereocidarid hudsouthensis* Cooke (1955, p. 89, pl. 18, figs. 1-4) has distinctly conjugate pores and, despite some deep, rudimentary-appearing (but probably only developing) upper plates, is not properly a stereocidarid. The species appears (from examined specimens) to belong to a genus close to both *Phyllacanthus* and *Prophyllacanthus*, but it has several features that set it apart so that it may not belong to either genus. *Phyllacanthus tysoni* Whitney and Kellum (1966, p.

244, pl. 2, figs. 4-6) and *Cidaris hemigranosus* Shumard (1860, p. 609) as illustrated by White (1883, pl. 18, figs. 2a-b) appear from descriptions and figures to be similar to, and perhaps the same as, Cooke's species. The sorting out of these species awaits further study.

Material. — The following Lambert and Sánchez Roig specimens, all in the Sánchez Roig collection, were not available for study: *Leiocidaris leoni* Lambert and Sánchez Roig, type no. 700, specimen 506A, and an unnumbered specimen, all tests; *Dorocidaris molineti* Lambert, no number given, a test; *Dorocidaris demujiensis* Sánchez Roig, type no. 120, two plates and one radiole; *Dorocidaris madrugensis* Sánchez Roig, type no. 106, apparently both plates and radioles.

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez (d)	PRI 29757	P. J. Bermúdez	—	1
Palmer 757	LSJU 53265	R. H. Palmer	—	1
Palmer 1117	PRI 29685	R. H. Palmer	—	5
Palmer 1117	LSJU 53247	R. H. Palmer	—	1
Palmer 1120	SUPTC 10248	R. H. Palmer	1	6
Palmer 1625	PRI 29686	R. H. Palmer	1	3
Palmer 2191	PRI 29687	R. H. Palmer	—	8
Palmer 2191	PRI 29748	R. H. Palmer	—	6
UCMP B-3254	UCMP 14463	R. H. Palmer	4	—
UCMP B-3404	UCMP 14461	R. H. Palmer	1	—
UCMP B-3408	UCMP 14462	R. H. Palmer	1	—
UCMP B-3469	UCMP 14464	R. H. Palmer	1	—
UCMP B-3499	UCMP 14465	R. H. Palmer	1	—
UCMP B-5231	UCMP 14501	R. H. Palmer	1	—
UCGS 29544	USNM 232517	N. Sohl <i>et al.</i>	7	66
USGS 30424	USNM 232518	N. Sohl <i>et al.</i>	1	1

Stratigraphic occurrence and localities. — Upper Cretaceous (including Habana Formation, Big Boulder Bed Member), Cuba; Upper Cretaceous (Maestrichtian), Jamaica.

Measurements. — See Table 13 for test measurements. Radioles 2.7-5 mm in diameter through shaft; nodular series 0.12-0.4 mm wide and spaced 0.12-1 mm apart, smallest and most closely spaced on adoral surface of shaft; minute (hair coat?) granules 0.04 mm in diameter; collar 2.2-3.45 mm long, 0.3-1.6 mm wider proximally than distally; milled ring 0.1-0.5 mm wider than proximal end of collar; base 1.9-2.2 mm long, width 0.9-1.6 mm less proximally than distally.

Prophyllacanthus eocenicus, new species

Plate 12, figures 1-4

Diagnosis. — Test large; areoles (at least on adapical plates)

Table 13. — Measurements of known tests and test fragments of *Prophyllacanthus leoni*.

Characters	UCMP 14465	UCMP 14461	UCMP 14464	UCMP 14462	UCMP 14463	USNM 232517	USNM 232518	PRI 29686
(in mm)								
HD	67	—	57	—	—	—	30 _o	—
VD	45	—	43	—	—	—	19	—
PerD	25	—	23	—	—	—	14.3 _o	—
ApSD	23.5	—	18	—	—	—	10.8 _o	—
IAmW	31	—	26	24	—	—	15	—
AmW	7	—	5	5	—	5	3.5	5.2
IAmPIW	18.5	16	15	14.5	13	13	9.5	8.6
ArW	11	10	10	10	8	8.5	6.5	6.3
MAW	4.5	3.5	3	3	2.5	2.5	1.5	1.2
AdrAW	3	2.5	2	1.5	2.5	2	1.5	1.3
PorAW	2	—	1.5	1.5	—	—	1.0	0.6
IPorAW	3	—	2.5	2.5	—	—	1.5	—
(as percentages)								
VD/HD	67	—	75	—	—	—	63 _o	—
AmW/IAmW	23	—	19	21	—	—	23	—
ArW/IAmPIW	59	62.5	67	69	62	65	68	73
MAW/IAmPIW	24	22	20	21	19	19	16	14
(as numbers)								
IAmPl:Col	8	—	7-8	—	—	—	5-6	—
AmPl:IAmPl	20-21	21	19	18	18	24-25 _a	15	—
IPorTub:AmPl	M+4-6	—	M+4-5	M+3	—	M+2-3	M+1	—

° = estimate (test crushed), _a = counts from adapical plate.

about 75 per cent width of interambulacral plate; tubercles large, perforate, those on upper plates partially and very faintly crenulate; scrobicular tubercles semicircular with sharply cut inner edges; pores subconjugate; radioles moderately stout, cylindrical, with up to 50 crenate ridges or series of small nodules. Collar short.

Description.—Test known from fragment consisting of two adapical interambulacral plates and a few adjoining ambulacral plates. Plates came from test estimated to have been at least 50 mm in horizontal diameter. Ambulacrum apparently sinuate, estimated about 13 per cent width of interambulacrum. Twenty-six ambulacral plates adjoining largest interambulacral plate, but fewer per plate expected at ambitus. Poriferous area only slightly depressed. Pores oval, subconjugate. Interporiferous area slightly narrower than one poriferous area on adapical plates. Marginal tubercles, with bases contiguous, completely filling interporiferous area; inner tubercles may have been present on plates at ambitus. Areoles of interambulacral plates only slightly depressed, about 75 per cent width of plate. Tubercles large, moderately high, faintly crenulate along upper edge of platform, perforate. Scrobicular tubercles large, semicircular, separated by small tubercles; inner edge sharply cut, and a ridge may have extended from scrobicular mamelon to this edge. Adradially, scrobicular tubercles abutting on ambulacrum. Median area narrow, 13 per cent of plate width, with room for only a few small tubercles outside scrobicular ring.

Radioles moderately stout (up to 4.8 mm wide), cylindrical, tapering distally to obtuse tips, probably up to 50 mm long. Shaft covered with small nodules in up to 50 more or less distinctly linear series or ridges, these fewer and more prominent distally. Surface between nodules on several fragments covered with fine, apparently anastomosed hairs. On other specimens, surface covered with minute nodules, probably remnants of hairs. Collars in few known basal fragments short and either of uniform width or slightly widened proximally. Milled ring weathered on extant specimens but appearing not to have been much wider than proximal end of collar. Base longer than collar and averaging 1.3 times wider distally than proximally. One or two fragments with faint irregularities along one edge of acetabulum (?crenulations). Best preserved acetabula smooth.

Discussion.—The crenulations on the upper tubercles of the only known test specimen are so shallow that they are barely perceptible. Nevertheless, they preclude assignment of the species to *Phyllacanthus* in which all tubercles are absolutely smooth.

It seems likely that *Prophyllacanthus eocenicus* is the evolutionary link between Cretaceous *Prophyllacanthus leoni* and Oligocene-Miocene *Phyllacanthus peloria* (Jackson) discussed later. It appears to differ from the former in having less distinct crenulations on the tubercles, shorter collars (2 to 3.5 mm long in *P. leoni*) and lower, smoother, less discrete nodules. From the younger species it is distinguished not only by the faint crenulations of its tubercles but by radioles that apparently were more slender (maximum width 8 mm in known radioles of *P. peloria*), probably shorter, and with shorter collars (to 2.5 mm long in *P. peloria*).

Several species described from European strata (e.g., *Cidaris belone* d'Orbigny (as illustrated by Cotteau in d'Orbigny, 1889-1894, pl. 303, figs. 22, 24) and *Cidaris subcylindrica* d'Archiac and *Cidaris striatogranosa* d'Archiac (Cotteau in d'Orbigny, 1889-1894, pl. 305, figs. 11-21) have radioles that have some resemblance to those of *P. eocenicus*, but whether they are in any way related to the Caribbean species is not possible to determine from the literature. A species closely related to *P. eocenicus* could be expected to have occurred somewhere in the Eocene Tethys, because in the Indian region there were both Cretaceous and Miocene species close to the Caribbean Cretaceous and Miocene phyllacanthid species.

Holotype.—SUPTC 10249a, a fragment of test collected by R. H. Palmer at Palmer locality 1003, Pinar del Rio Province, Cuba.

Paratypes.—LSJU 53248, 53249; PRI 29633, 29634; SUPTC 10249b-e, 10250, 10251.

Material.—

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Palmer 491	PRI 29633	R. H. Palmer	—	2
Palmer 1003	SUPTC 10249a (holotype)	R. H. Palmer	1	—
Palmer 1003	SUPTC 10249b-e	R. H. Palmer	—	3
Palmer 1064	LSJU 53249	R. H. Palmer	—	8
Palmer 1082	SUPTC 10250	R. H. Palmer	—	13
Palmer 1085	PRI 29634	R. H. Palmer	—	47
Palmer 1085	SUPTC 10251	R. H. Palmer	—	1
Palmer 1085	LSJU 53248	R. H. Palmer	—	9

Stratigraphic occurrence and locality. — Eocene *sensu stricto* and upper Eocene (Jabaco Formation), Cuba.

Measurements. — Largest interambulacral plate in holotype (an adapical fragment of test): 12 mm wide, 11 mm high; ArW 9 mm; MAW 2 mm; AdrAW 1 mm; AmW (adapical) 3.4 mm; IPorAW 1 mm.

Radioles: width of extant specimens commonly 3.4-3.8 mm (range 1.8-4.8 mm); longest fragment 30.5 mm long, from radiole estimated to have been at least 50 mm long; small nodules or crenate ridges mostly 0.15-0.3 mm wide and spaced 0.15-0.3 mm apart; minute nodules or hairs commonly 0.04-0.08 mm in diameter (range 0.02-0.12 mm); collar 0.2-1.35 mm long and averaging 0.125 mm wider proximally than distally; milled ring not more than 1 mm wider than proximal collar; base 0.5-1.2 mm long and 1.2-1.4 times wider distally than proximally.

Genus **PHYLLACANTHUS** Brandt

Phyllacanthus peloria (Jackson)

Plate 13, figures 1-7

1922. *Cidarid peloria* Jackson, p. 16, pl. 1, figs. 2-5.

Description. — Known test fragments from moderately large to large cidaroids, probably at least 60 mm in horizontal diameter. Pores widely separated, conjugate. Interporiferous area twice width of one poriferous area; median suture not depressed. Marginal tubercles in regular series, bases contiguous or nearly so; inside marginals on each plate, one tubercle about same size as marginal; no bare areas. On most complete fragment (BM E75629), oral and adapical surfaces slightly flattened but not incurved; fourteen ambulacral plates per interambulacral plate at ambitus.

Six interambulacral plates per column in BM E75629 (originally may have been seven), all separated by at least double row of scrobicular tubercles. Areoles large, only slightly depressed, 69 per cent width of plate at ambitus in BM specimen, 68 to 83 per cent in other two specimens (isolated plates: AMNH 18564/3; USNM 232515). Tubercles moderately high, smooth. Median area width less than 20 per cent width of plate. Scrobicular tubercles prominent and semicircular to elliptical; outer edge well marked; inner edge cut sharply to scrobicule. A few small tubercles covering rest of plate to sutures.

Ambital radioles large, robust, some as wide as 8.5 mm; some fragments from radioles probably at least 75 to 90 mm long. Shaft in large radioles scarcely tapered throughout but slightly flattened, ending in rounded tip; in smaller radioles, shaft gradually tapered to obtuse or acute tip. Surface of shaft covered with as many as 50 more or less distinct, longitudinal series of small, closely spaced nodules, these joined at tip of radiole to form seven or more prominent ridges. Minute nodules, probably remnants of hair coat, between and up sides of nodules. Collars short and scarcely widened toward inconspicuous milled ring. Width of base 20 to 27 per cent less proximally than distally.

Discussion. — *Phyllacanthus priscus* Brito and Ramires (1974a, p. 264, pl. 1, figs. 1, 5-7) was described from specimens collected in the lower Miocene (Pirabas Formation) of Brazil. The illustrated radioles bear some resemblance to radioles of *Phyllacanthus peloria*, but the interambulacral plates in the test specimens, especially the specimen in figure 1, are considerably wider than in specimens here referred to *P. peloria*.

P. peloria was one of the largest cidaroids in the Caribbean Miocene (*Prionocidaris spinidentatus* (Palmer) may have been larger). Specimens of both species have been found in some localities. Tests of the two can be separated most easily on the basis of the width of the median area of interambulacral plates (distinctly narrower in *P. peloria*) and numbers of interporiferous tubercles on ambulacral plates (fewer in *P. peloria*). The radioles of *P. spinidentatus* are grossly spinulose and thus easily distinguished from the nodulose and ridged phyllacanthid radioles.

P. peloria appears to have been part of an evolutionary continuum in the Caribbean dating back to the Cretaceous, descending from *Prophyllacanthus leoni* through *Prophyllacanthus eocenicus*. Differences between the three species were discussed under *P. eocenicus*.

The radioles of *P. peloria* resemble to considerable extent those of the following Oligocene and Miocene species: *Phyllacanthus titan* Fell from New Zealand, *Phyllacanthus duncani* Chapman and Cudmore and *Phyllacanthus clarkii* (Chapman and Cudmore) from Australia. However, *P. titan* apparently was a much larger species, its radioles reaching 200 mm in length and 10 mm in width, and

Table 14. — Selected test characters of four species of *Phyllacanthus*. Measurements for *P. peloria* and *P. imperialis* were taken from specimens; those for *P. duncani* and *P. clarkii* were either copied from Philip (1963, p. 209, 215) or were determined by me from his pl. 23, fig. 4 (holotype of *P. duncani duncani*) and pl. 25, fig. 3 (lectotype of *P. clarkii clarkii*).

Characters	<i>P. peloria</i>	<i>P. duncani</i>	<i>P. clarkii</i>	<i>P. imperialis</i>	
HD (mm)	≈53	43	59	41-50	51-60
AmW/IAmW (%)	23	16	15	16-19	18-22
ArW/IAmPIW (%)	69	57	47	70-83	66-79
MAW/IAmPIW (%)	17	29	43	18-25	12-21
IPorAW/PorAW	2	<1.0	2 _a	1.5-2	1.3-2
IAmPI:Col	6	6-7	9	5-6	5-6
AmPI:IAmPI (ambital)	14	19	15-16	16-17	14-19

_a = approximately.

differences in test characters help to distinguish *P. peloria* from the other two species (Table 14). Radioles of *P. peloria* also resemble those of *Phyllacanthus imperialis* (Lamarck), which lives in the Indopacific, and at least one test specimen of *P. peloria* (BM E75629) is nearer the test of *P. imperialis* than those of the fossils mentioned above (see Table 14). More test specimens of *P. peloria* are needed, however, to make a careful comparison with the Recent species.

Fossil radioles and a few test specimens similar to those of Recent *P. imperialis* have been reported from Miocene and younger strata over much of the Indo-Pacific from Madagascar (Cottreau, 1908, p. 183, pl. 5, fig. 10) and Pakistan (Duncan and Sladen, 1882-1886, p. 284, pl. 45, fig. 13) to Fiji (H. L. Clark in Ladd and Hoffmeister, 1945, p. 313, pl. 15, fig. 13). Philip (1963, p. 203) gave a more complete listing of occurrences.

Material. — The 72 radiole fragments from NYAS-AMNH localities 20, 56, 58, 105, noted by Jackson (1922, p. 17), were not seen. These are part of the AMNH collections but could not be found during my visit there.

Locality	Catalogue Number	Collector	Number of specimens Test	Radiole
Martin-Kaye GR222699	BM E75629	P. Martin-Kaye	1	—
NYAS-AMNH 56 (type-locality)	AMNH 18564/ 2, 3*, 4, 5, x	C. A. Reeds <i>et al.</i>	1	4
Palmer 1028	PRI 29636	P. J. Bermúdez	—	20
Palmer 1041	PRI 29637	R. H. Palmer	—	11
Palmer 1042	ANSP 50988	R. H. Palmer	—	1
Palmer 1042	PRI 29638	P. J. Bermúdez	—	9
Palmer 1042	PRI 29639	R. H. Palmer	—	53

Material. — (continued)

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Palmer 1044	ANSP 50973	R. H. Palmer	—	4
Palmer 1045	PRI 29640	R. H. Palmer	—	8
Palmer 1090	PRI 29641	R. H. Palmer	—	8
Palmer 1107	PRI 29642	R. H. Palmer	—	16
Palmer 1262	PRI 29643	P. J. Bermúdez	—	20
Palmer 1262	PRI 29644	R. H. Palmer	—	241
Palmer 1452	PRI 29645	R. H. Palmer	—	30
Palmer 1627	PRI 29646	R. H. Palmer	—	12
Palmer 1719	PRI 29647	R. H. Palmer	—	16
USGS 17212	USNM 232515	H. R. Bergquist	1	22
USGS 19795	USNM 232516	C. W. Cooke <i>et al.</i>	—	1

* = holotype.

Stratigraphic occurrence and localities. — lower to upper Oligocene and Miocene(?), Cuba; lowest Miocene (Antigua Formation), Antigua; Oligocene to lower Miocene (Lares Formation), Puerto Rico.

Measurements. — See Table 15 for measurements of test specimens. Radioles: maximum length (estimated) 75 to 90 mm; maximum width of shaft (4-22 mm above collar) to 8.5 mm, more commonly 4-6 mm; nodular ridges on proximal half of shaft 0.2-0.4 mm wide and spaced 0.3-0.8 mm apart; minute nodules (remnants of hairs?) about 0.08 mm in diameter; neck 3-6 mm long; collar 1-2.5 mm long, of uniform width or either 0.2-0.5 mm wider or slightly narrower proximally; milled ring not more than 3 mm wider than proximal end of collar; base 1-2 mm long and 1.1-1.5 times wider distally than proximally.

Family **PSYCHOCIDARIDAE** IkedaGenus **TYLOCIDARIS** Pomel**Tylocidaris bermudezi**, new species

Plate 14, figures 1-4

Diagnosis. — Test small. Ambulacrum unknown. Areoles large. Tubercles smooth and imperforate or, on adapical plates, apparently perforate. Scrobicular tubercles prominent. Radioles short, fusiform (widest below midpoint of shaft) or almost cylindrical. Shaft having longitudinal series of peaked nodules or dentate ridges and, over entire surface, minute (hair coat?) nodules. Tips acute to obtuse and simple or slightly widened and finely coronate. Collar short, distal limits oblique; acetabulum smooth.

Description. — Two interambulacral plates, only known test specimens, parts of small test. Areoles not much depressed, two-

Table 15.—Measurements of test specimens of *Phyllacanthus peloria*.

Characters	AMNH 18564/3 (hypotype)	BM E75629	USNM 232515 (adapical fragment)
(in mm)			
HD	—	53.	—
VD	—	—	—
PerD	—	—	—
ApSD	—	—	—
IAmW	—	26	—
AmW	—	6	—
IAmPIW	17	14.5	14.3
ArW	11.6	10	11.8
MAW	3	2.5	1.8
AdrAW	2.4	2	0.7
PorAW	—	1.5	—
IPorAW	—	3	—
(as percentages)			
VD/HD	—	—	—
AmW/IAmW	—	23	—
ArW/IAmPIW	68	69	83
MAW/IAmPIW	18	17	13
(as numbers)			
IAmPl:Col	—	6	—
AmPl:IAmPl	—	14	19
IPorTub:AmPl	—	M+1	—

° = estimated from measurements of Recent *P. imperialis* having IAmPIW of 14.5 mm.

thirds or more of plate width. Tubercles moderately high, smooth, apparently imperforate on one plate, perforate on other. Median and adradial areas of about equal width, narrow. Scrobicular tubercles nearly round, higher on outer edge, sloping inward to scrobicula, and with edges contiguous. Few small, crowded tubercles outside scrobicular ring.

Known radioles up to 20 mm long and 4.5 mm wide, varying from almost cylindrical to distinctly fusiform. Widest part of shaft in fusiform radioles below midpoint. Tips typically simple and acute to obtuse but slightly widened and coronate in several specimens. Shafts having 11 to 21 longitudinal series of peaked nodules, these commonly coalesced to form dentate ridges; series narrowest and most closely spaced on adoral surface of radiole. Surface between and up sides of nodules and ridges covered with minute nodules, probably remnants of hairs. Collars short, about same width throughout and about one-third to one-half as long on adoral side of radiole as on adapical. Milled ring only slightly wider than collar. Bases

about same length as collar or slightly shorter and varying little, if at all, in length from one surface to another. Acetabulum smooth; imperforate in most specimens but appearing perforate in several.

Discussion. — *Tylocidaris bermudezi*, from the Caribbean Eocene, is most similar to *Tylocidaris macneili* Cooke (1959, p. 12, pl. 1, figs. 3-5), one of three tylocidarid species from the Paleocene of the eastern and southern United States. *T. bermudezi*, however, has some perforate tubercles (all imperforate in *T. macneili*), more acutely tapered tips on the fusiform radioles, and wider ridges on all the radioles than in *T. macneili*. *T. bermudezi* differs similarly from *Tylocidaris* sp. A (Cretaceous of Cuba), discussed next, and may be its descendant.

Tylocidaris bermudezi is named for Dr. Pedro J. Bermúdez, who collected many of the known specimens.

Holotype. — SUPTC 10252a, a radiole collected by R. H. Palmer at Palmer locality 1102, Pinar del Rio Province, Cuba.

Paratypes. — ANSP 16682; LSJU 53250-53258; PRI 29700-29711; SUPTC 10252b-r, 10253.

Material. —

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Bermúdez 110	PRI 29700	P. J. Bermúdez	—	3
Bermúdez 154	PRI 29701	P. J. Bermúdez	—	2
Bermúdez 185	PRI 29703	P. J. Bermúdez	—	3
Bermúdez 246	PRI 29704	P. J. Bermúdez	—	9
Bermúdez 261	PRI 29705	P. J. Bermúdez	—	3
Bermúdez 324	PRI 29706	P. J. Bermúdez	—	4
Bermúdez 337	PRI 29707	P. J. Bermúdez	—	18
Bermúdez 526D	PRI 29708	P. J. Bermúdez	—	4
Bermúdez 604	PRI 29709	P. J. Bermúdez	—	9
Palmer 52	LSJU 53250	R. H. Palmer	—	1
Palmer 53	LSJU 53251	R. H. Palmer	—	2
Palmer 72	LSJU 53252	R. H. Palmer	—	1
Palmer 165	PRI 29702	R. H. Palmer	—	5
Palmer 491	PRI 29710	R. H. Palmer	—	8
Palmer 727	LSJU 53253	R. H. Palmer	—	1
Palmer 1003	LSJU 53254	R. H. Palmer	—	12
Palmer 1027	LSJU 53255	R. H. Palmer	—	9
Palmer 1082	LSJU 53256	R. H. Palmer	—	3
Palmer 1085	LSJU 53257	R. H. Palmer	—	8
Palmer 1102	PRI 29711	R. H. Palmer	—	65
Palmer 1102	SUPTC 10252a (holotype)	R. H. Palmer	—	1
Palmer 1102	SUPTC 10252b-r	R. H. Palmer	2	15
Palmer 1228	LSJU 53258	R. H. Palmer	—	1
Palmer 1640	SUPTC 10253	R. H. Palmer	—	13
Palmer 1640	ANSP 16682	R. H. Palmer	—	7

Stratigraphic occurrence and locality. — middle Eocene (Loma Candela Formation) and upper Eocene (Jabaco Formation), Cuba.

Measurements. — Test: in largest known plate, IAmPIW 5 mm; ArW 3.5 mm (70% IAmPIW); MAW = AdrAW 0.8 mm. Other plate, IAmPIW 4.4 mm; ArW 3 mm (68% IAmPIW); MAW 0.9 mm; AdrAW 0.5 mm.

Radioles: Holotype, 13 mm long, 5×4 mm wide; widest part of shaft 7 mm from tip, 3 mm from collar; 18 ridges at widest point; nodules or ridges up to 0.8 mm wide; minute nodules up to about 0.08 mm wide; collar 1 mm long on adoral surface, 1.5 mm on adapical surface, 3.1 mm wide distally, 3.1 mm proximally; milled ring 3.2 mm wide; base 1.2 mm long, 3 mm wide distally, 2 mm proximally.

Other radioles, up to 20 mm long and 4.5 mm wide; nodules or ridges commonly 0.3-0.55 mm wide (range 0.15-1.1 mm), usually spaced 0.4-0.55 mm apart transversely (range 0.25-0.8 mm), and projecting up to 0.3 mm; minute nodules (remnants of hairs?) 0.04-0.08 mm wide; collars commonly 0.3-0.8 mm long (range 0.3-1.5 mm); bases usually 0.4-0.8 mm long (range 0.4-1.1 mm).

Tylocidaris sp. A

Plate 14, figures 5-8

Description. — Only known test specimen (interambulacrum and adjoining half ambulacra) from small test (HD 15 mm), neither flattened nor incurved at adoral and adapical margins. Apical system slightly wider than peristome. Ambulacra nearly straight. Eleven ambulacral plates adjoining one interambulacral plate at ambitus. Pores closely spaced, slightly oblique, nonconjugate. Interporiferous area twice as wide as one poriferous area. Marginal tubercles in regular series; on each plate, one inner tubercle about same size as marginal and, on some plates, one or two additional small tubercles. Five interambulacral plates per column, all separated by at least a single row of scrobicular tubercles. On interambulacral plate at ambitus, areole width 52 per cent of plate width. Tubercles low; platforms smooth; mamelons large and imperforate. Median area width 31 per cent of plate width. Scrobicular tubercles almost round, not prominent. Uniform, slightly smaller tubercles crowded on rest of plate to sutures.

Known radioles short, slender and fusiform to ovate. Widest

part about midpoint of shaft or slightly below it. Tips acute to obtuse. Shafts with 10 to 20 longitudinal series of peaked nodules, these either discrete or joined into dentate ridges and narrowest and most closely spaced on adoral surface of radiole. Surface between and up sides of dentations and nodules covered with minute nodules, apparently remnants of hairs, or, in one radiole (SUPTC 10254), a dense coat of short hairs. Short neck apparent on some specimens. Collars very short (less than 0.5 mm long), about same width throughout. Milled ring only slightly wider than collar. Base slightly longer than collar. Acetabulum of some radioles completely smooth, but faint indications of crenulations along one edge in several specimens; a few apparently perforate.

Discussion.—*Tylocidaris* sp. A, from scant known material, appears similar to *Tylocidaris macneili* Cooke, from the Paleocene of Alabama. The Cuban test fragments are from a larger test than the holotype of *T. macneili* (USNM 56266a) but otherwise agree well with it. The broadest of the Cuban radioles (PRI 29712) has a wider tip than the broadest radioles of *T. macneili*, possibly because of erosion. The slender radioles of both species are nearly comparable, the main differences being larger nodules on the shafts and shorter collars in the Cuban specimens (in *T. macneili*, the nodules are up to 0.25 mm wide and collars are up to 1.5 mm long). Although the Cuban and Alabaman species probably are not the same due to differences in age, the latter may be a descendant of the former. More Cuban specimens in good condition, particularly of the ovate radioles, will be needed to determine definitely that *T.* sp. A is distinct; meanwhile, it is left without a specific name.

The Cuban Eocene species *Tylocidaris bermudezi* also may be a descendant of the Cuban Cretaceous form. It differs from the latter in having narrower ovate radioles with longer tips, longer radiole collars, entirely smooth acetabula on all the radioles, slightly coarser hairs and apparently perforations on some of the tubercles of the test.

Material.—

Locality	Catalogue Number	Collector	Number of specimens	
			Test	Radiole
Palmer 757	SUPTC 10254	R. H. Palmer	—	4
Palmer 812	PRI 29712	R. H. Palmer	—	1
Palmer 812	SUPTC 10255	R. H. Palmer	—	4
Palmer 832	SUPTC 10256	R. H. Palmer	—	1
Palmer 895P	LSJU 53259	R. H. Palmer	—	1
Palmer 2191	PRI 29713	R. H. Palmer	—	6
UCMP B-3290	UCMP 14502	R. H. Palmer	1	—

Stratigraphic occurrence and locality.—Upper Cretaceous (including Habana Formation, Big Boulder Bed Member), Cuba.

Measurements.—Test (UCMP 14502): HD (estimated) 15 mm; VD 10.5 mm; ApSD (estimated) 5.5 mm; PerD 5 mm; IAmW 8.5 mm; AmW 4 mm; IAmPIW 4.8 mm; ArW 2.5 mm (52% IAmPIW); MAW 1.5 mm (31% IAmPIW); ADrAW 0.8 mm; PorAW 2 mm; IAmPl:Col 5; AmPl:IAmPl 11.

Radioles: longest complete specimen 14 mm long but some fragments probably from radioles up to 20 mm long; shafts 2.1-6.1 mm wide; dentate ridges and nodules usually 0.3-0.6 mm wide, narrowest on oral surface of radiole, and commonly spaced 0.4-0.6 mm apart transversely (range 0.25-0.9 mm); hairs and minute nodules (remnants of hairs?) usually 0.04 mm in diameter; neck, if present, 0.3-0.6 mm long; collars 0.2-0.4 mm long, 1.75-2.1 mm wide, nearly same width throughout; bases 0.5-0.6 mm long, 0.3-0.5 mm narrower proximally than distally.

Tylocidaris? sp. B

1957. *Cidaris* sp. aff. *C. californicus* W. B. Clark, Osten, p. 578, pl. 63, fig. 5.

Discussion.—Osten referred to *Cidaris* sp. aff. *C. californicus* several radioles that he collected from the Barranquín Formation (Taguarumo Member) of Venezuela. He described them as “almost spherical-ellipsoids,” the shaft of a typical specimen measuring 21 mm long, 11 mm at the widest and 3 mm at the neck; the surface was “covered with granules small and round near the base, growing coarser toward the point”; some granules were “aligned longitudinally.” His figured specimen appears to be similar to tylocidarid radioles and resembles especially the Cuban Late Cretaceous specimens here described as *Tylocidaris* sp. A, except that it is larger than the latter.

Osten mentioned that the Venezuelan radioles were similar to some from the Cretaceous of Mexico that he had seen in collections at Stanford University and that were labelled (mistakenly, he thought) *Cidaris dixonii* Cotteau and to others from the Jurassic of California that were described as *Cidaris californicus* Clark (1893, p. 36, pl. 6, figs. 1a, 1b). His specimens also appear similar to one or two of those from the Aptian of Mexico that Maldonado-Koerdell (1953, p. 20, pl. 1, figs. 4-7) referred to *Cidaris galeotti* Desor. However, Maldonado-Koerdell also illustrated (1953, pl. 1, figs. 12-16)

other bulbous radioles from the same site that appear not to belong to the Order Cidaroida. If the species to which the Venezuelan radioles belong is truly tylocidarid, the Upper Cretaceous Cuban species might be a descendant.

Incertae Sedis
Indeterminate genus A
Plate 14, figures 9-11

Description. — Test unknown. Known radiole fragments up to 32 mm long, 3.5 mm wide, tapered. Only intact tip acute. Shafts with up to 13 prominent, serrate or crenate ridges; four to six of these on adoral surface of radiole narrowest and most closely spaced. Surface otherwise smooth, lacking any indications of hairs. Collars short, 1 mm wider proximally than distally or of uniform width. Milled ring up to 0.2 mm wider than proximal end of collar. Bases about same length as collar or a little longer and about 0.2 mm narrower proximally than distally. Acetabulum, where intact, smooth.

Discussion. — The radioles assigned to indeterminate genus A have the general shape of radioles described here as *Palmerius roberti* n. gen., n. sp., but they do not have either the indications of a dense hair coat or the crenulate acetabula of the latter. Also, they are Miocene in age whereas *P. roberti* is Eocene. They are unlike the ridged radioles referred here to *Prionocidaris* species, having serrations that vary in size only through gradual diminution toward the tip of the radiole; also, they were not found in any of the localities from which known specimens of *Prionocidaris* were collected.

The only other cidaroid material collected with specimens of indeterminate genus A (in Palmer locs. 932, 1393, 1593) were radioles that are distinctly eucidarid and have been referred here to *Eucidaris madrugensis*. In the Recent record, there is no precedent for referring radioles with distinctly serrate ridges to *Eucidaris*. Fell (1954) associated radioles that are ridged but have typical eucidarid tips with an Eocene *Eucidaris* from New Zealand. Two ridged radioles, also with eucidaridlike tips, were here questionably referred to *E. madrugensis*. However, the radioles of indeterminate genus A are not at all like the last mentioned two specimens, and they certainly are not like typical eucidarid radioles. The only more or less intact tip on these radioles appears to have been acute, and the tipless specimens have a gradual taper such as often characterizes

acute-tipped radioles. Eucidarid radioles, on the other hand, taper slightly but typically end bluntly in tips with a rosette. There is no indication whatever of hairs on the radioles of indeterminate genus A, whereas eucidarid radioles have dense hair coats. No specimens from the four localities listed below could be considered intermediate between the tapered, ridged radioles of indeterminate genus A and typical eucidarid radioles. Since the former do not appear similar to those of any other genus, they remain generically indeterminate.

Material. —

Locality	Catalogue Number	Collector	Number of radiole specimens
Bermúdez 299	PRI 29666	P. J. Bermúdez	3
Palmer 932	PRI 29735	R. H. Palmer	6
Palmer 1393	PRI 29736	R. H. Palmer	2
Palmer 1593	PRI 29737	R. H. Palmer	5

Stratigraphic occurrence and locality. — middle Miocene (Güines Formation, Yumurí limestones), Cuba.

Measurements. — Radioles: maximum length of fragments 32 mm; maximum width 3.5 mm; serrate ridges (up to 13) commonly 0.3-0.4 mm wide (range 0.2-0.7 mm); collar 0.6-0.9 mm long, up to 2.6 mm wide, uniform width throughout or not more than 0.1 mm wider proximally; milled ring not more than 0.2 mm wider than proximal collar; base 0.6-1.3 mm long, not more than 0.2 mm narrower proximally than distally in the few specimens with intact acetabula.

Indeterminate genus B
Plate 14, figure 12

Description. — Test unknown. Largest of radiole fragments from radioles probably up to 25 mm long, moderately wide, and slightly tapered. Shaft in widest (proximal) fragment bearing 11 longitudinal series of high nodules or low spinules, most joined into ridges. Surface between and up sides of ridges covered with minute (hair coat?) granules. Collar apparently about 1.5 mm long, scarcely widened proximally. Milled ring eroded. Base missing.

Discussion. — The fragments assigned to indeterminate genus B bear some resemblance to the ridged radioles of several species of *Prionocidarid* (*P. cojimarensis*, *P. spinidentatus* and *P. katherinae*), but all the latter species are Miocene in age. They have more

widely spaced ridges and higher, sharper protuberances on the ridges than radioles here referred to the Cretaceous species *Stereocidaris* sp. B but may belong to that species.

Material. — USNM 243089, seven fragments of radioles collected at USGS locality 30066, Jamaica, by N. D. Sohl and others.

Stratigraphic occurrence and locality. — Upper Cretaceous, Jamaica.

Measurements. — Radioles from which known fragments came: length approx. 20-25 mm; width up to 3.5 mm; ridges approx. 0.5 mm wide, spaced 0.5-1 mm apart; minute granules approx. 0.04-0.06 mm wide; collar approx. 1.5 mm long, 2.5 mm wide at distal end, up to 0.5 mm wider proximally.

SYNTHESIS

Table 16. — Fossil and Recent Cidaroida of the Caribbean area, with depth ranges of the Recent species.

	Cret.	Pal.	Eo.	Olig.	Mio.	Plio.	Pleist.	Rec.	Depth ranges for Recent species (m)
<i>Histocidaris</i>									
<i>sanchezi</i>			X						
<i>H. sp. indet.</i>					X				
<i>H. nuttingi</i>								X	320-415
<i>H. sharreri</i>								X	570
<i>Poriocidaris</i>									
<i>purpurata</i>								X	750-1800
<i>Stereocidaris</i>									
<i>S.?</i> sp. C.		X							
<i>S. sp. B</i>		X							
<i>S. sp. A</i>			X	X					
<i>S. ingolfiana</i>								X	300-1750
<i>Cidaris cubensis</i>			X						
<i>C. bermudezi</i>					X				
<i>C. abyssicola</i>								X	200-400
<i>C. blakei</i>								X	315-420
<i>C. rugosa</i>								X	130-540
<i>Calocidaris</i>									
<i>palmeri</i>					X				
<i>C. micans</i>								X	200-330
<i>Tretocidaris</i>									
<i>anguillensis</i>					X				
<i>T. bartletti</i>								X	140-625
<i>Stylocidaris</i>									
<i>affinis</i>								X	30-1000
<i>S. lineata</i>								X	100-500
<i>Palmerius roberti</i>			X						
<i>Eucidaris</i>									
<i>madrugensis</i>					X	X?	X?		
<i>E. tribuloides</i>						X?	X	X	0-450
<i>Prionocidaris</i>									
<i>loveni</i>			X	X					
<i>P. spinidentatus</i>				X	X				
<i>P. clevei</i>					X				
<i>P. cookei</i>					X				
<i>P. cojimarensis</i>					X				
<i>P. katherinae</i>					X				
<i>Fellius foveatus</i>			X						
<i>Prophyllacanthus</i>									
<i>leoni</i>		X							
<i>P. eocenicus</i>			X						
<i>Phyllacanthus</i>									
<i>peloria</i>				X?	X				
<i>Tylocidaris sp. A</i>	X								
<i>T.?</i> sp. B	X								
<i>T. bermudezi</i>			X						
Indeterminate									
genus B	X								
Indeterminate									
genus A					X				
Total species per time unit	6	1	8	2-3	12	1-2?	1-2	12	

EVOLUTION

In the known Caribbean cidaroid fauna, there are 11 named genera. There are indications of evolutionary trends between the oldest and youngest species in eight of these genera. In the only endemic genus, *Calocidaris*, the Recent species *C. micans* (Mortensen) undoubtedly is the descendant of Miocene *C. palmeri* n. sp. Between these two, the evolutionary changes were minor: the wall between the pores of the test became higher and narrower; most of the crenulations of the tubercles were lost, at least in adults; areoles on adoral interambulacral plates became confluent; and the radioles developed a few more ridges and became longer. With respect to the wall and crenulations, the young of *C. micans* resemble the adults of *C. palmeri*.

Tretocidaris also is represented in the Caribbean by both Recent and Miocene species, *T. bartletti* (A. Agassiz) and its probable ancestor, *T. anguillensis* n. sp., respectively. The latter is known from only two tests. If they are typical of the species, evolution of the test from *T. anguillensis* to *T. bartletti* would have involved some narrowing of the ambulacra, heightening and narrowing of the wall between the pores, and an increase in the number of ambulacral plates per interambulacral plate.

At least two of the three species of *Cidaris* now living in the Caribbean may have had Caribbean ancestors. The bladelike tips of the radioles of *C. cubensis* Lambert in Lambert and Thiery (Eocene) resemble those of the Recent species *C. blakei* (A. Agassiz) and suggest an evolutionary sequence, although the test of *C. cubensis* is unknown and such widened tips are not known from Caribbean strata younger than Eocene. On the basis of the few known fossil radioles, evolution from Eocene to Recent species would have involved an increase in width of the shafts and the flattened tips of the radioles.

The small "hoof" and large number of serrate ridges on some of the radiole fragments from Puerto Rico that are questionably referred to *Cidaris bermudezi* n. sp. indicate that these fragments may belong to another species and may be in the line of descent of the Recent species *Cidaris abyssicola* (A. Agassiz). The type-specimens of *C. bermudezi* do not lend themselves to speculation about a possible descendant. However, Cuban and Puerto Rican test speci-

mens referred to *C. bermudezi* have ambulacra that are wider than is usual in *Cidaris*. In a Puerto Rican test specimen that was extracted from the same small (about 4 cm³) block of limestone from which I also removed the *abyssicola*-like radiole fragments (mentioned above) and that thus probably also is referable to *Cidaris*, the pores are almost conjugate. This difference in pore spacing between fossil and Recent species is the sort noted above in *Calocidaris* and *Tretocidaris*.

Eucidaris tribuloides (Lamarck), now living in the Caribbean, dates back to the Pleistocene and possibly also the Pliocene in this area. The fossil species *Eucidaris madrugensis* (Sánchez Roig), which occurred in the Caribbean as early as the Miocene, probably was ancestral to *E. tribuloides*. Since *E. madrugensis* apparently appeared in the Caribbean before closure of the Isthmus of Panama, it may also have been ancestral to *Eucidaris thouarsii* (Valenciennes), living in the eastern Pacific.

During evolution from *E. madrugensis* to either of the Recent species, the whorls of large nodules that occurred on radioles apparently from adults of the fossil species would have disappeared except in small juveniles, collars of the radioles would have been lengthened, and there would have been a slight increase in the number of interambulacral plates per column. In *E. tribuloides* there apparently would also have been reduction in width of the primary areoles in relation to interambulacral plate width and a slight reduction in the number of ambulacral plates per interambulacral plate. In *E. thouarsii*, the peristome would have become consistently wider than the apical system, except in small specimens (up to 11 mm HD).

There are two modern Caribbean species of *Histocidaris*. One of these, *H. nuttingi* Mortensen, may have descended from the Caribbean Eocene species *Histocidaris sanchezi* (Lambert in Lambert and Thiery) through *Histocidaris* sp. indet. from the Caribbean Miocene. Regarding radioles, evolutionary changes necessary between the Eocene and Miocene species include reduction in number of ridges and in size of the sparse spinules, shortening of the collar and flattening of the adoral surface of the shaft. No real difference could be found between the few radiole specimens of the Miocene species and radioles of *H. nuttingi*. Test specimens collected with the Eocene radioles all are fragmental so it is hard to base compari-

sons on them, but apparent differences between tests of the Eocene and Recent species also are minor: compared to *H. sanchezi*, *H. nuttingi* has marginal tubercles that are less uniform in size, a few more inner tubercles in the ambulacra, as well as wider median areas on interambulacral plates.

There are two Caribbean species of *Tylocidaris*, *T. bermudezi* n. sp. of Eocene age and an indeterminate Cretaceous species that may be of the same lineage. Differences between the two, which may represent evolutionary changes, include the apparent presence of some perforate tubercles on the test and more acutely tapered tips and wider ridges on the radioles of the younger species.

In the remaining genera, only in the phyllacanthids is there a sequence of Caribbean species that suggests evolutionary change. *Prophyllacanthus leoni* (Lambert and Sánchez Roig in Sánchez Roig) from the Cretaceous and *Prophyllacanthus eocenicus* n. sp. (Eocene), distinguished from species of *Phyllacanthus* by some crenulations of tubercles on the test, are here assigned to a new genus. By the Eocene, these crenulations had almost disappeared, the collar of the radioles had shortened, and the ridges on the shaft of the radioles had become lower and more or less crenate instead of bearing nodules that were sharply peaked and covered with fine serrations. In the Miocene species *Phyllacanthus peloria* (Jackson), the last of this apparent lineage, the tubercles all were smooth and the radioles had widened and apparently lengthened.

In sum, evolution in the cidaroids, as reflected in the Caribbean fauna, apparently proceeds slowly, only minor changes occurring over millions of years. One change noted here in *Calocidaris*, *Tretocidaris* and *Cidaris* was a heightening and narrowing of the wall between the pores of the test, enough so that what were subconjugate pores in Miocene species became nonconjugate in the Recent species. This observation may provide support for arguments against use of modern genera for fossil species. However, even in living species of a few genera (e.g., *Tretocidaris*), there may be either nonconjugate or subconjugate pores, and in species with nonconjugate pores, the young may have small pores separated by a wall that appears proportionately wider and lower than in the adult. In many genera, the pores are incontestably and invariably nonconjugate or conjugate; in these, considerable systematic weight can be given to the pores. But it should be recognized that in the

Subfamily Cidarinae, the nature of the wall between the pores is variable and is not a good taxonomic character. If other characters of the test and radioles that distinguish a modern genus are found also in a fossil (even in the absence of pedicellariae), it seems better to use the modern genus than either to clutter the literature with genera named solely for fossils or, as has been done too often in the past, to lump fossils into *Cidaris*, *Dorocidaris* (nonconjugate pores) or *Leiocidaris* (conjugate pores).

As Mortensen (1928b, p. 16) indicated, crenulation of the primary tubercles of the interambulacra appears to be a primitive feature, at least when considering Jurassic to Recent cidaroids. Reduction and loss of crenulation was one of the evolutionary changes noted during this study, in *Calocidaris* between the Miocene and present, and in the phyllacanthid series between the Cretaceous and Miocene species. Such crenulations are one feature which, although absent in the adult of a species, may be evident in the young.

In *Eucidaris*, the loss of whorls of large nodules in radioles of the adult during the late Tertiary was noteworthy. Whorls remaining in radioles of the very young of living eucidarids remind us of the ancestry of these forms. As Phelan (1970, p. 13) noted, radioles of very small *E. tribuloides* (the same holds true in *E. thouarsii*) are ornamented with spinules that, as the individual grows, change into rounded nodules. The radioles of the young also are banded with light and dark areas, and the conversion into nodules is accomplished first in the dark bands. Uniformity in nodules and in pigmentation (dark) of the radioles are attained more or less coincidentally. In the fossil eucidarid radioles, there are no visible signs of banding now, but perhaps the distinctive whorls of large nodules are reflections of pigmental differences in the radioles of the adults of the fossil species.

PALEOBIOGEOGRAPHY AND BIOSTRATIGRAPHY

For many of the fossil Caribbean cidaroids recorded in this paper, there appear to be affinities with extra-Caribbean species, fossil and Recent, some of which are found as far away as India, Japan, Australia, and Hawaii. Ekman (1953, p. 63) and others also have noted a resemblance between tropical Atlantic and Indo-West Pacific faunas and between Caribbean-Gulf and European faunas (review in Berggren and Aubert, 1975, p. 138). There is

little doubt that dispersals have occurred between these areas. The distributions of known Caribbean cidaroids and their possible allies suggest possible routes.

Modern Seas

Studies of modern faunas indicate that even the present wide expanse of the Atlantic Ocean can be crossed by some marine species. When continents bordering this ocean were closer together (as the sea-floor spreading concept suggests), successful dispersals between them should have been more frequent than now.

Although there have been reports of dispersals of organisms by rafting of newly metamorphosed juveniles on floating seaweed or other material (Ekman, 1953, p. 61; Fell, 1967, p. 320; Mortensen, 1933, p. 416), transport of planktonic larvae in surface currents probably has always been the predominant means of dispersal across ocean deeps. In the Atlantic now, westward-flowing North and South Equatorial Currents might carry larvae from the eastern Atlantic to northern South America or the Caribbean. A west-east Equatorial Undercurrent flows between Brazil and Africa, and the Gulf Stream and North Atlantic Drift could transport larvae north from the Caribbean and eastward across the Atlantic.

Velocities range between 0.5 to 1.2 km/h for the North Equatorial Current, 1.3 to 2.3 km/h for the South Equatorial Current, 1.8 to 5.4 km/h for the Equatorial Undercurrent, and 0.7 to 1.3 km/h for the North Atlantic Drift, so a planktonic larva would require about 17 to 21 weeks to cross the 3700 km from Cape Verde to Barbados, 9 to 21 weeks for an east-west crossing over the 4625 km between the Gulf of Guinea and Brazil or 5 to 15 weeks west-east in the undercurrent, and 17 to 43 weeks to pass west to east over the 4000 km between Cape Hatteras and the Azores (Scheltema, 1971, p. 22).

Although cold-water invertebrates apparently do not remain planktonic more than about 58 days (Ekman, 1953, p. 240) or 68 days (Thorson, 1961, p. 460, fig. 1), there is increasing evidence that larvae of many tropical marine invertebrate species, representing almost all the major phyla, are capable of delaying metamorphosis for extended periods, long enough for successful crossing in any of the currents mentioned above (Scheltema, 1971, p. 23-24). Although I did not find references that include data on delay of metamorphosis

in tropical cidaroids, geographic distributions of several echinoids indicate trans-Atlantic dispersals in relatively recent times.

As noted by Fell (1967, p. 321), *Tripneustes ventricosus* (Lamarck) and *Echinometra lucunter* (Linn.) both are known from West Africa, Brazil, the Caribbean area and north to Bermuda, suggesting west-east dispersal in the equatorial currents and Gulf Stream. Both have also been reported from Ascension Island, although Pawson (1978, p. 20) considered the record for *T. ventricosus* doubtful and created a new subspecies for specimens of *E. lucunter* from Ascension Island. *Eucidaris tribuloides* (Lamarck) is found in the Azores and Cape Verde Islands, Gulf of Guinea, northern coast of South America, throughout the Caribbean and Gulf of Mexico and north to Bermuda, i.e., along the paths of the currents mentioned above. *Poriodidaris purpurata* (Wyv. Thomson) is found in the Caribbean, as far north as southern Iceland and in the eastern Atlantic down to the Canary Islands (Phelan, 1970, p. 16 recorded the Caribbean specimens) and *Stereocidaris ingolfiana* Mortensen occurs from the Caribbean north to Denmark Strait and south to the Cape Verde Islands, suggesting transport of larvae of these species in the Gulf Stream and North Atlantic Drift. *Stylocidaris affinis* (Philippi) also is a Caribbean and amphi-North Atlantic species and occurs in the Mediterranean as well. That the latter three are more tolerant of cold than the other nine cidaroid species now living in the Caribbean is also indicated by their depth ranges (Table 16).

Dispersal of cidaroids across the Pacific is a different matter. There are east-west North and South Equatorial currents and a faster west-east Equatorial Countercurrent, the latter attaining a maximum velocity of about two knots (1.4 km/h) according to charts or perhaps twice that, as noted by Garth (1966, p. 444). However, distances from western America to the nearest islands to the west are enormous, roughly 6000 km from Central America to the Marquesas and 5000 km between the west coast of Mexico and the Hawaiian Islands.

Some fish and invertebrate species have managed to cross even the East Pacific Barrier, including about two per cent of the species and 14 per cent of the genera of asteroids, ophiuroids and echinoids (Ekman, 1953, p. 74), but the echinoids do not include any cidaroid

species (Mortensen, 1928b, p. 529). Dispersals across the Pacific seem less likely, therefore, to account for similarities between faunas of Caribbean and Indo-Pacific areas than dispersals through, or bidirectional dispersals from, the ancient Tethys Sea. This study indicates the latter mode may have been the primary one for cidaroids. However, the lack of updated generic assignments, the unsatisfactory descriptions of many Tethys species, and continuing progress in Caribbean biostratigraphy and global paleogeography, limit my suggestions of dispersal routes to working hypotheses. Because continental positions and oceanic currents and temperatures were different in the past, these variables must be considered in any theories of dispersal of fossil species.

Paleogeography

Many proponents of continental drift believe that a single supercontinent, named Pangaea by Wegener (1924), existed at the beginning of the Mesozoic. There is no consensus on the alignment of the present continents within this mass. Agreement is best for lands now bordering the Atlantic. In the reconstruction of Bullard *et al.* (1965, fig. 1), slightly modified by Smith and Hallam (1970, fig. 1), Dietz and Holden (1970, fig. 2) and others, South America abuts Africa, its northeast corner in the Gulf of Guinea; North America touches both Africa and Eurasia, its entire east coast fitted around the northwestern bulge of Africa and its northeast border aligned against Greenland and western Europe; and the western portion of the north coast of South America overlaps present Central America.

Other major land masses (Antarctica, India-Seychelles, Madagascar, Australia, New Zealand) were grouped to the east and south of Africa and south of South America. Common to most models of how all these fit together is the alignment of both southern Australia and eastern India with Antarctica (the latter in about its present position) and of Madagascar with southwestern India, but there are differences in the position of Madagascar that in turn affect the alignment of India and Antarctica with Africa. In some reconstructions (*e.g.*, du Toit, 1937; Smith and Hallam, 1970), Madagascar lies off the coast of Kenya, western India is off Somalia and Arabia, a portion of Antarctica abuts Mozambique, and the Antarctic peninsula is between the southern tips of Africa and South

America. Other models (*e.g.*, Tarling, 1972; Barron *et al.*, 1978), have Madagascar in a more southern position off Mozambique and the Antarctic peninsula on the west side of the tip of South America.

Most reconstructions of Pangaea include a large, wedge-shaped ocean (Tethys; rarely Paleotethys) between northeastern Africa and Eurasia. A portion of the west coast of India and western or northwestern Australia apparently also bordered on this sea.

North Atlantic. — The oldest known Caribbean cidaroids lived during the Late Early Cretaceous. The North Atlantic at this time was already a sizeable ocean. It had begun to open in Late Triassic or Early Jurassic time, about 180 to 200 m.y. ago, and by the end of the Cretaceous had attained about 60 to 67 per cent of its present width south of the Azores Ridge, according to magnetic anomaly lineation patterns, although it was closed or nearly so to the north (Funnell and Smith, 1968, p. 1330; Pitman and Talwani, 1972, p. 641, fig. 6).

The Caribbean crust may have derived from differential movement between North and South America or may have been emplaced from the Pacific. By the Early Cretaceous, it probably was almost entirely formed or fully emplaced. It covered an area equivalent to the present Caribbean Sea (Le Pichon and Fox, 1971, p. 6304; Saunders *et al.*, 1973, p. 1107), although the north-south width may have increased somewhat and then decreased as a result of plate movements between the Late Cretaceous and Miocene (Holcombe and Moore, 1977, p. 47).

During the Eocene, the land corridor across the northern limits of the North Atlantic was disrupted. Major rifting around Greenland started about 80 m.y. ago to the west and 60 m.y. ago to the east, and Eurasia separated from Greenland at Spitsbergen in about mid-Eocene time, allowing relatively cold water from the Norwegian Sea to enter the North Atlantic for the first time (Pitman and Talwani, 1972, p. 641; Phillips and Forsyth, 1972, p. 1583).

South Atlantic. — Rifting between Africa and South America started in the latest Jurassic (Dietz and Holden, 1970, p. 4948) or Early Cretaceous (Maxwell *et al.*, 1970, p. 464; Le Pichon and Hayes, 1971, p. 6292; Larson and Ladd, 1973, p. 209), the southern South Atlantic opening first. Until the Turonian, there apparently was a land connection between Africa and the northeastern corner

of Brazil. In Late Cenomanian and Early Turonian time, a shallow epicontinental sea extended through North Africa, allowing faunal exchange between the South Atlantic and Tethys, and an epicontinental sea may have existed in South America between the Sergipe Basin and the Caribbean (Reyment and Tait, 1972, p. 67, fig. 3), but not until the late early Turonian (Reyment and Tait, 1972, p. 90, fig. 9) or mid-Turonian (Premoli-Silva and Boersma, 1977, p. 629) was there direct communication between the South and North Atlantic.

Indian Ocean. — Initial separation of Antarctica, Madagascar, India and Australia from Africa and Antarctica from South America has been variously dated but probably occurred in Late Jurassic (Barron *et al.*, 1978, p. 445) or Early Cretaceous time (Le Pichon and Heirtzler, 1968, p. 2114). India probably separated from Antarctica about 140 m.y. ago and from Madagascar in the Late Cretaceous, about 100 m.y. ago (Barron *et al.*, 1978, p. 446). It moved northward, and by the late Eocene its northern border was either nearing southern Eurasia (Le Pichon, 1968, p. 3691; Dietz and Holden, 1970, p. 4952) or had already collided with it (Heirtzler *et al.*, 1968, p. 2135). What had been the original Tethys was gradually replaced by the Indian Ocean.

Tethys-Mediterranean Sea. — Some, including Dietz and Holden (1970, fig. 4), show the original Tethys extending westward as far as Spain, although apparently there is some disagreement over the western borders of the sea. During the Jurassic, when continents were separating, Eurasia began to drift westward and dextrally with respect to Africa, and Africa moved eastward and rotated sinistrally. These movements resulted in the opening of Tethys to the Atlantic but at the same time effected progressive closure of the original Tethys (Dietz and Holden, 1970, p. 4948; Hsü and Bernoulli, 1978, p. 946). During the Cretaceous, movement of Africa continued to be sinistral (Dietz and Holden, 1970) or became dextral during the Santonian (Hsü and Bernoulli, 1978). The latter authors (p. 947) suggested complete collision of Africa with Europe during the latest Eocene, elimination of the western Mediterranean-area basins at the same time, but formation of new basins and continued connection between the Atlantic and Indo-Pacific during the late Oligocene and Miocene. Formation of the eastern margin of the Mediterranean Sea has been dated as early Miocene (Ruggieri, 1967, p. 284; Berggren and Hollister, 1974, p. 157; Hsü,

Montadert, *et al.*, 1978, p. 1059), although, according to Hsü, Montadert, *et al.* (1978, p. 1060), there may have been repeated transgressions into the Mediterranean from the Indo-Pacific until middle Miocene time.

Several factors led to a salinity crisis in the Mediterranean during the late Miocene: drainage from European rivers into the sea was blocked at the time the eastern margin closed; northward drift of Africa closed the Betic and Rif straits after the beginning of the Messinian; there was a general drop in sea level during the late Miocene; and although there apparently was some influx of Atlantic water into the Mediterranean during the Messinian, it was not sufficient to offset normal evaporation (Hsü, Montadert, *et al.*, 1978, p. 1061). By the end of the Messinian, the Mediterranean was largely dry but refilled with North Atlantic water within a relatively short time at the beginning of the Pliocene. These phenomena were verified by deep sea drilling (Hsü, *et al.*, 1973; Hsü, Montadert, *et al.*, 1978, and others cited by them) but were suggested much earlier (Stefanini, 1924, p. 840).

Antarctic Seas. — Australia remained attached to Antarctica throughout the Cretaceous. By the middle Eocene, it had moved northward enough so that there was a considerable sea between it and Antarctica, although the South Tasman Rise and Campbell Plateau did not subside enough for strong, deep sea currents to develop until middle or late Oligocene time, about 20 to 30 m.y. ago (Kennett *et al.*, 1975, p. 1167) or early Miocene (Hayes and Frakes, 1975, p. 937).

Paleocurrents

North Atlantic. — Berggren and Hollister (1974, p. 166-167, fig. 15), in a synthesis of the work of many others, noted that early in the Cretaceous currents flowed westward through Tethys, continuing across the Atlantic as the North Equatorial Current. Part of this current, as it reached the Caribbean area, turned northward north of Cuba to form the Gulf Stream; part was deflected northward into the Gulf of Mexico and from there into the epicontinental sea that extended through the west-central part of North America to the Arctic; and part continued westward into the Pacific. A branch of the Gulf Stream flowed northeastward across the Atlantic, through the Tethys Sea to the Himalayan area and on to the Indo-Pacific region.

Organic-rich sediments found during deep sea drilling at a number of widely separated sites in the Atlantic and Caribbean (sites and authors given by Saunders *et al.*, 1973, p. 1098, and Lancelot and Seibold, 1977, p. 1225) indicate that from early Barremian to Cenomanian or Coniacian-Santonian time circulation through the Caribbean and western Atlantic was extremely weak and that there were periods of stagnation. According to Saunders *et al.* (1973), lack of carbonaceous sediments in Pacific cores of the same age "demands a barrier between the Pacific and Caribbean separating the bottom water regime of the two basins," and the presence of radiolarians in Lower Cretaceous sediments of the Caribbean and Pacific and their absence in the Atlantic indicate there probably was a weak flow of surface waters from the Pacific into the Caribbean.

Strong deep-water circulation in both the Caribbean and North Atlantic apparently started in Santonian time and probably was activated by separation of South America from Africa along the transcurrent margins, which allowed exchange of bottom waters between the North and South Atlantic (Saunders *et al.*, 1973, p. 1099; McCoy and Zimmerman, 1977, p. 1071). At the same time, the Central American barrier, whatever it was, subsided; there is evidence that from the Late Cretaceous to early Miocene time the east-west currents through the Caribbean were stronger than at present (Holcombe and Moore, 1977, p. 44). Late Cretaceous regressions reduced the epicontinental sea through North America, and a clockwise gyre formed in the Gulf of Mexico, the exiting water joining the Gulf Stream as at present (Berggren and Hollister, 1974, p. 159).

Separation of Greenland from Eurasia also contributed to the initiation of major deep-water circulation in the North Atlantic (Ewing and Hollister, 1972, p. 971; Berggren and Hollister, 1974, p. 167, 172). Currents thus generated may have been strong by the late Eocene (Pimm and Hayes, 1972, p. 966), although there is some evidence that mass exchange between the Norwegian Sea and the North Atlantic was not possible until the end of the Miocene (Schrader *et al.*, 1976, p. 1207).

Circulation through the Caribbean weakened in early to middle Miocene time, probably as a result of the constriction of Tethys, development of the Lesser Antilles, and closure of the Panamanian isthmus. The isthmus was probably sufficiently emergent by the

middle Miocene to impede movement of water into the eastern Pacific (Holcomb and Moore, 1977, p. 52). With closure of the isthmus in the early Pliocene, all circulation between the Atlantic and Pacific ceased, and all water entering the Caribbean was diverted northward.

South Atlantic.—Paleocirculation in the South Atlantic has been outlined by McCoy and Zimmerman (1977, p. 1068-1072, pl. 6). Until some time between the Aptian and Albanian-Cenomanian, when a deep-water gap opened between the eastern end of the Falkland Plateau and the southern tip of Africa, there was only surface circulation between the South Atlantic and the Pacific and Indian oceans. The land bridge between northeastern Brazil and Africa prevented even shallow-water exchange between the South and North Atlantic until the Turonian. The Rio Grande Rise and Walvis Ridge formed an effective barrier to significant circulation between the Argentine-Cape Basin and the Brazil-Angola Basin until, in the mid-Campanian, this sill began to subside. However, during the Turonian there was shallow inflow from Tethys into the northern basin through the North African epicontinental sea. In the northern basin, a surface geostrophic gyre developed and expanded from the Late Cretaceous to the middle Eocene. After the northern land bridge opened, there was northwesterly outflow from the basin along the Brazilian coast and a southwesterly inflow along the southern border of the African bulge. By the late Eocene, there was a strong influx of cool bottom water into the southern basin. During the Oligocene, south-moving North Atlantic and South Atlantic deep waters were able to flow from the Brazil Basin to the Argentine Basin through the Hunter Channel and the Rio Grande Gap, but northward flow of bottom waters was still impeded. By the close of the Miocene, the modern circulation system existed.

Indian Ocean-Tethys.—Throughout the Cretaceous, with Australia still attached to Antarctica, no major land mass interrupted east-west currents from the Pacific into Tethys. During the Oligocene, however, Australia had moved far enough north to restrict circulation (Kennett *et al.*, 1975, p. 1166). India, moving northward toward Eurasia, must also have influenced patterns of circulation through Tethys during the Cretaceous and Eocene.

Antarctic Seas.—With subsidence of the South Tasman Rise and Campbell Plateau south of Australia and New Zealand, as well

as of the Drake Passage south of South America, a strong, deep Circum-Antarctic Current developed during middle to late Oligocene time, about 25 to 30 m.y. ago (Kennett *et al.*, 1975, p. 1167) or early Miocene (Hayes and Frakes, 1975, p. 937). This current effectively prevented intermixing of south polar and tropical waters (Savin *et al.*, 1975, p. 1506.).

Paleotemperatures of Oceans

Cretaceous. — Throughout the Cretaceous, temperatures of the oceans were more uniform and warmer than at present. According to Berggren and Aubert (1975, p. 77), "the North Atlantic was essentially a subtropical province with chalks being deposited in the Labrador Sea, coastal Greenland and Denmark." Deep-sea temperatures were at least 16° to 17°C during the Santonian (Lowenstam, 1964, p. 245) and 14° to 15°C during the Campanian and early Maestrichtian, as compared to present bottom-water temperatures of 2° to 3°C; surface-water temperatures probably were also about 14° to 15°C but dropped over 2°C from middle to late Maestrichtian time and 1.5°C more from the late Maestrichtian to early Danian, and there were more pronounced decreases at the bottom (Saito and Van Donk, 1974, p. 160).

Paleocene-Eocene. — Studies of the distribution of microplankton indicate marked cooling episodes in the Central and North Atlantic during the middle Paleocene and middle Eocene, although there was warming between these periods, and the middle Eocene cooling may have been followed by a relatively stable and generally warmer climate in the late Eocene (Haq *et al.*, 1977, p. 3871-3873). However, according to Savin *et al.* (1975, p. 1503), oxygen isotope studies indicate that after the end of the middle Eocene time there was a period of rapid cooling, and bottom temperatures in the northern latitudes dropped to 7°C by the end of the Eocene. As mentioned under "Paleocurrents," after final separation of Eurasia and Greenland about mid-Eocene, relatively cold water from the Norwegian Sea began to enter the North Atlantic. Provincialization of faunas began in the Paleocene (Berggren and Hollister, 1974, p. 161; Haq *et al.*, 1977, p. 3974). Surface and bottom temperatures varied sympathetically, but temperature changes apparently were less marked in equatorial regions (Savin *et al.*, 1975, p. 1506).

Temperature changes of similar nature apparently occurred at high southern latitudes. Surface temperatures south of New Zealand

on the Campbell Plateau were estimated by Shackleton and Kennett (1974, p. 751) to have been 18° to 20°C during the late Paleocene and early Eocene and to have dropped in a series of steps during the Eocene, the most dramatic drop (to about 7°C) near the Eocene-Oligocene boundary, while temperatures of waters at about 1000 m depth were about 1°C lower than at the surface.

Oligocene - Miocene. — According to Shackleton and Kennett (1974, p. 752), the dramatic temperature drop at the Eocene-Oligocene boundary marked the onset of a deep-sea circulation that is dominated, as today, by the formation of near-freezing bottom water around Antarctica; surface waters at the Antarctic coast probably were near freezing at the beginning of the Oligocene, and there likely were glaciers at sea level; and there were fluctuations to warmer temperatures in the early and middle Miocene, but the thermal structure of the present oceans was probably established at the beginning of the Oligocene.

Savin *et al.* (1975, p. 1504-1506) found that in other oceans there was a rise of about 3°C in bottom temperatures between the end of the Oligocene and end of the early Miocene; there was a dramatic drop of 3°C within a period of 2 to 3 m.y. early in middle Miocene time, probably due to glaciation; and surface temperatures decreased sympathetically with the bottom temperatures in high latitudes but apparently in low latitudes, more or less synchronously, surface temperatures were actually increasing, suggesting a change in latitudinal solar energy distribution. The latter change may have been the result of the development of the strong Circum-Antarctic Current that prevented intermixing of south polar and tropical waters.

There apparently was an upset in shallow-water carbonate deposition from the middle Miocene to the Pliocene (indicated by absence of limestones throughout the Pacific during that period), which might be attributed not only to a fall in sea level (a result of Antarctic glaciation) but also to the return of the vast quantities of evaporated Mediterranean water to the world's oceans as fresh water (Adams, 1976, p. 58).

Paleobiogeographic Patterns

Stereocidaris. — There is only one species of *Stereocidaris* in the Caribbean today, but the genus flourishes in the Indo-Pacific. The distribution of the fossil Caribbean, Gulf and eastern United States

stereocidarids — Venezuela (possibly *Stereocidaris*? sp. C), Mexico (*Cidaris mullerreidi*) and Texas (*Cidaris texanus*) in the Early Cretaceous; Jamaica (*Stereocidaris* sp. B) in the Late Cretaceous; Cuba in the Late Cretaceous (*Stereocidaris* sp. B) and Eocene (*Stereocidaris* sp. A); and Alabama and New Jersey (*Cidaris splendens*) in the Paleocene — suggests dispersal by currents that moved along the northern coast of South America and up into the Gulf of Mexico and, after regression of the North American epicontinental sea in the Late Cretaceous, through the Gulf and northward. One of the species of *Stereocidaris* in the Mediterranean-area Tethys may have been the source of larvae that reached the Caribbean-Gulf area. Brazil may have been an alternate source. *Cidaris branneri* from the Brazilian Cretaceous is much like *C. mullerriedi* (Mexico) and *C. texanus* (Texas) as well as the Caribbean species. Although the Sergipe Basin, where *C. branneri* lived, apparently was cut off from the North Atlantic during the Early Cretaceous, there are two other possible dispersal routes: the hypothetical epicontinental seaway between Sergipe and the Caribbean and a route around the southern tip of South America and north along the western coast of South America. Dispersals by the latter would have been facilitated by the moderate temperatures at high latitudes and the lack of strong west-east currents around Antarctica during the Cretaceous. Some early Turonian vascoceratid cephalopods apparently moved along this route as far as Peru and Mexico (Reyment and Tait, 1972, p. 90). Because there may have been weak currents from the eastern Pacific into the Caribbean during the Early Cretaceous, dispersal into the Caribbean may have been possible.

A difficulty in theorizing descent of the Recent Caribbean species *Stereocidaris ingolfiana* from the Caribbean Eocene *S. sp. A* is the lack of any indication of "wings" on the fossil radioles. The close resemblance between *S. ingolfiana* and the Recent Indo-Pacific species *Stereocidaris indica* suggests that a fossil species in the Mediterranean or Indian area may have been the ancestor of both and the focus for bidirectional radiation. The two modern species, although now separated by barriers, are not only close morphologically but live at far greater depths than all the other stereocidarid species discussed by Mortensen (1928b).

Tylocidaris. — This genus did not survive the Eocene. The distribution pattern of fossil Caribbean-Gulf-western Atlantic species of *Tylocidaris* — possibly Venezuela (*T.*? sp. B) and Mexico (radioles similar to the Venezuelan specimen) in the Late Cretaceous; Cuba in the Late Cretaceous (*T.* sp. A) and Eocene (*T. bermudezi*); and Alabama (*T. macneili*, *T. salina*) and New Jersey (*T. walcotti*) in the Paleocene — is similar to that of the stereocidarids. If there were true tylocidarids in Venezuela and Mexico early in the Cretaceous, the origin of those species would be even more uncertain than that of the stereocidarids. The numerous European *Tylocidaris* species were younger (Late Cretaceous and Paleocene). Species having bulbous radioles (generic affinities uncertain) lived in California during the Jurassic (*Cidaris californicus* from Taylorsville) and Lower Cretaceous (*Cidaris tehamaensis* from Tehama County), but even if the latter is tylocidarid, it occurred so far north in California it is unlikely that its larvae could have reached any currents that flowed into the Caribbean from the eastern Pacific during the Early Cretaceous.

Prophyllacanthus and *Phyllacanthus*. — No phyllacanthids are found now in the Caribbean or Atlantic, but three fossil Caribbean species are known and a number of modern species exist in the Indo-Pacific. Similarities between *Prophyllacanthus leoni* and *Phyllacanthus sindensis*, from Caribbean Maestrichtian and Pakistani upper Paleocene strata, respectively, suggest that these species may be closely related. If so, there may have been west-east dispersals from the Caribbean across the warm North Atlantic and through Tethys to western Sind. Alternatively, both *P. leoni* and *P. sindensis* may have derived from a western Tethys species. Although I have not seen the illustrations of the species, *Dorocidaris africanus* Lambert (1909, pl. 1, figs. 5-6) from the Maestrichtian of Algeria may warrant consideration in this regard. That dispersals to Sind from either the Caribbean or the Mediterranean area were possible, at least during the Paleocene, is indicated by similarities between faunas of the Caribbean, Mediterranean and Sind (Adams, 1967, p. 199, citing others).

As mentioned in the "Systematics" section, *P. leoni* appears to have been the start of a Caribbean phyllacanthid lineage that continued through *Prophyllacanthus eocenicus* (Eocene) to *Phyllacanthus peloria* (late Oligocene-early Miocene). More or less parallel

evolution of the Pakistani species and dispersals eastward from Sind may account for the Recent Indo-Pacific species *Phyllacanthus imperialis*. A massive cylindrical radiole from the Miocene of Sind (Duncan and Sladen, 1882-1886, pl. 45, fig. 13) appears much like some belonging to *P. peloria* as well as radioles of *P. imperialis*.

Another possibility for the origin of *P. leoni* is *Rhabdocidaris brasiliensis* from the Middle Albian of Sergipe, Brazil. Although the Brazil-Africa land bridge north of Sergipe probably prevented northward dispersal to the Atlantic, alternate routes mentioned under *Stereocidaris* may have been open.

Fellius. — *Fellius foveatus* from Caribbean middle and upper Eocene strata is the only known species in this genus. It closely resembles *Rhabdocidaris zitteli* from the upper Eocene of Egypt and lower Eocene of Qatar (possibly also British Somaliland) and *Porocidaris anomala* from upper Eocene strata of Libya and Sind. Also, the middle(?) Eocene species *Rhabdocidaris pouechi* of Europe resembles the other species, particularly the British Somaliland form. Since India-Pakistan probably remained close to northeastern Africa early in the Eocene, it seems possible that *P. anomala* derived from *R. zitteli*. The occurrence of *P. anomala* as far west in Tethys as Libya suggests westward dispersal along the northern coast of Africa for that species. *F. foveatus* may also have derived from *R. zitteli*, either by dispersal through the Mediterranean or, because conditions south of Africa were equable during the Eocene, down the east coast of Africa, into the South Atlantic and northward.

Palmerius. — The only known species in this genus is *Palmerius roberti* from the upper Eocene strata of Cuba. The test of *P. roberti* is unknown, but excellently preserved radioles suggest genetic ties to *Stylocidaris? fusispina*, living in Japanese seas. Because *S.? fusispina* has tests with pores unlike typical *Stylocidaris* pores and radioles that are unique, Mortensen (1928b, p. 384) questioned the assignment of the species to *Stylocidaris*. Test specimens of the Eocene species and more and older specimens of *S.? fusispina* are needed for close comparison, but these species may be related or even congeneric, and Tethyan relatives may be found.

Prionocidaris. — The only modern prionocidarids live in the Indo-Pacific, but the genus was particularly well represented in the Caribbean from the Eocene to the Miocene. The middle and late Eocene species *Prionocidaris loveni* of St. Bartholomew, Cuba and

Jamaica apparently persisted into the early Oligocene in Cuba. Its polymorphic radioles resemble those of *Prionocidaris baculosa*, now living in the Indo-Pacific, enough to suggest that the two species had genetic ties. There may have been west to east dispersal from the Caribbean with *Leiocidaris canaliculata*, which lived in western Sind during the late Eocene, as the Tethyan link. However, along with other differences, *P. baculosa* lacks the narrow interporiferous area that is so distinctive in the fossil species.

Of the six species of *Prionocidaris* that lived in the Caribbean during the Oligocene and(or) Miocene, three (*P. cojimarensis*, *P. katherinae* and *P. clevei*) had distinctly verticillate radioles that resemble those of *Prionocidaris verticillata* (Recent, Indo-Pacific) and of *Prionocidaris praeverticillata* from lower Miocene strata of Kenya and western Sind. The resemblance between the early to middle (or late) Miocene species *P. cojimarensis* and *P. praeverticillata* is particularly close. The latter may have been the focus for bidirectional radiation from Tethys. West-east dispersal from the Caribbean in the early Miocene would seem less likely because of the lowered temperatures in the North Atlantic. As Stephenson (1968, p. 560) indicated, fragments of radioles from the Pliocene of Indonesia assigned by Lambert and Jeannet (1935) to *Leiocidaris* (*Plococidaris*) *verticillata* may represent an intermediate between *P. praeverticillata* and *P. verticillata*. *Cidaris vafellus* from the Miocene of Angola is a possible (but not very convincing) link between *P. praeverticillata* and *P. cojimarensis*; its known radioles resemble one (but not the most characteristic) of the three forms of radioles of *P. cojimarensis*.

P. katherinae (late early to middle Miocene or Pliocene) appears to be related to *P. cojimarensis*, *P. praeverticillata* and (especially in the distinctly verticillate arrangement of the spinules on its radioles) the Recent species *P. verticillata*. It may have come to the Caribbean in a separate dispersal through Tethys from *P. praeverticillata*, or it may have derived from early stocks of *P. cojimarensis*. The latter case, however, would require reduction in size from *P. praeverticillata* to *P. cojimarensis* and then increase in size from *P. cojimarensis* to *P. katherinae*, and this seems unlikely.

The third Caribbean species from lower Miocene strata with verticillate radioles, *P. clevei*, is known only from the lower Miocene of Anguilla. It is much smaller than *P. cojimarensis*, *P. katherinae* and *P. praeverticillata*, and its radioles are so much

more tightly whorled than those of the other three species that it is hard to conceive genetic ties between it and any of the others. Still, there is the possibility that *P. praeverticillata* gave rise to it. This would not preclude derivation of *P. cojimarensis* and *P. katherinae* also from *P. praeverticillata*. To suggest descent of *P. cojimarensis* and *P. katherinae* from *P. clevei* after the latter had derived from *P. praeverticillata* would seem less sensible since that would require considerable diminution, followed by increase in size of the descendant species within a relatively short time.

I have no suggestion for a possible antecedent of another Caribbean prionocidarid, the middle Miocene species *Prionocidaris cookei*, which ranged up into Florida. The species most similar to this species appears to be *Prionocidaris hawaiiensis*, known only from the Recent in Hawaii. Unless *P. cookei* and its descendants spread westward from the Caribbean into the eastern Pacific and across the formidable East Pacific Barrier to Hawaii, there must be an unknown Tethyan ancestor of *P. cookei* from which larvae dispersed eastward into the Central Pacific as well as westward to the Caribbean. As *P. cookei* lived at a time when Tethys was closing, it is less likely that dispersal was east from the Caribbean into Tethys and then into the Indo-Pacific.

Prionocidaris spinidentatus lived in the ancient Caribbean possibly as early as the early Oligocene but certainly in early and middle Miocene (?to Pliocene) time. It is strikingly like the Recent Indo-Pacific species *Prionocidaris bispinosa*. It is also similar to *Prionocidaris* sp. (early Miocene, Brazil), *Cidaris* sp. (middle Oligocene-early Miocene, western Sind), *Cidaris adamsi* and *Cidaris avenionensis* (both early Miocene, Malta), *Leiocidaris sismondai* (middle Miocene, Sardinia), and *Phyllacanthus sundaica* (Tertiary, Java). If the early Oligocene date for *P. spinidentatus* is correct, this species and its descendants may have spread first from west to east (from the Caribbean to Sind) and then may have undergone bidirectional radiation from Sind, back through the Mediterranean area as well as eastward to the Pacific. Temperatures in the North Atlantic already were low, however, so west-east dispersals from the Caribbean probably were not likely.

Histocidaris.—Only two histocidarid species now live in the Caribbean, but there are many in the Indo-Pacific. The genus was represented in the Caribbean during the early, middle and late

Eocene, apparently by a single species, *Histocidaris sanchezi*. The lineage may have continued through an indeterminate Miocene species to *Histocidaris nuttingi* (Recent, Caribbean). The latter is similar to two Recent Indo-Pacific species of *Histocidaris*, *H. recurvata* and *H. formosa*, suggesting that these three Recent species had a Tethyan ancestor in common, or there was west to east dispersal from one of the Caribbean fossil species. There are Mediterranean fossils that appear much like *H. sanchezi* but are younger, e.g., the Oligocene species *Cidaris vepres* and the Miocene species *Histocidaris oranensis*. Older species with slender, sparsely spinulose radioles (e.g., *Cidaris spinulosa* and *Cidaris phillipsi*, both from the Jurassic) occurred in Tethys, but these seem less like *H. sanchezi*. A revision of Tethyan cidaroids by someone with access to specimens and full access to the older literature may find a more likely pre-Eocene Tethyan link.

Cidaris. — This genus is now limited to the Caribbean, North Atlantic and Mediterranean. There apparently were species of *Cidaris* in the Caribbean in both the late Eocene (*C. cubensis*) and Miocene (*C. bermudezi*). Only *C. cubensis* has features (bladelike radioles) that are especially distinctive. Such radioles are found also in the recent Caribbean species *Cidaris blakei*. The latter may be a descendant of *C. cubensis*. There are records of Miocene and Pliocene species with radioles similar to those of *C. blakei* from the Mediterranean area (see discussion of *C. cubensis*). These may have been descendants of *C. cubensis*, following west to east dispersals from the Caribbean during the Eocene. Apparently, no species with flattened radioles is known from the eastern Atlantic, but this may be due to incompleteness of the fossil record. Even if none existed there prior to dessication of the Mediterranean, stocks from the Miocene Mediterranean species must have exited to shores or islands of the eastern Atlantic during the crisis and then reentered the sea when it refilled during the Pliocene, eventually dying out there. If the *C. cubensis* lineage died out in the Caribbean after the Eocene, dispersals to the Caribbean from some eastern Atlantic stock might account for *C. blakei*.

The widened, flattened radioles of *C. cubensis* also resemble those of *Stylocidaris? chapmani*, from the Oligocene of southeastern Australia, but until tests of the Caribbean fossil become known, there is no way to know if this similarity represents a real affinity

between species or a case of parallel evolution in one feature of otherwise dissimilar species.

Tretocidar. — There are only two Recent species of *Tretocidar*, *T. bartletti* of the Caribbean and *T. spinosa* of St. Helena (in the South Atlantic). *Tretocidar anguillensis*, which lived in Anguilla during the early Miocene, may be a species whose ancestors migrated out of the Mediterranean. Its close resemblance to *Cidar melitensis* from Burdigalian limestones of Malta suggests a genetic link between the two. As mentioned in the discussion of *T. anguillensis*, it seems less likely that this species derived from *C. melitensis* than that they had a common ancestor. Whatever the source, stocks of an ancestor of *T. anguillensis* probably reached the shores of Northwest Africa or outlying islands. From there larvae may have been swept to the Caribbean where evolution through *T. anguillensis* to *T. bartletti* took place. Other larvae from the same stocks may have been dispersed southward along the African coast and eventually to St. Helena.

Cidar melitensis resembles the Recent species *Stylocidar affinis* closely enough that Mortensen (1928b, p. 335) suggested that the latter might be a descendant of *C. melitensis*. *S. affinis* appears to have considerable temperature tolerance; it lives in the relatively cold Mediterranean and along the European coast as well as in the Caribbean, Gulf of Mexico and as far north as Bermuda, and at depths up to 1000 meters. If stocks of *C. melitensis* reached European shores during the Mediterranean crisis, it is possible they evolved there to *S. affinis* and that dispersals from these populations back into the Mediterranean (when it refilled) as well as across the Atlantic to the Caribbean-Gulf area and northward may have resulted in the present distribution of *S. affinis*. The direction of surface currents in the Mediterranean make it less likely that *S. affinis* evolved there and then dispersed across the Atlantic. *T. bartletti* is limited to warm waters, indicating its lineage may have had less cold tolerance than that of *S. affinis*. This, in turn, suggests that it is not likely that eastward dispersals from *T. anguillensis* across the cold Miocene North Atlantic could account for either *C. melitensis* of Malta or the eastern Atlantic and Mediterranean populations of *S. affinis*.

Eucidaris. — *Eucidaris tribuloides*, which is found on the African coast as well as in the Caribbean, is one of the five modern

species in this genus. Mayr (1954, p. 3) suggested that these species, distributed over most tropical and subtropical seas, all arose by allopatric speciation from a population whose Atlantic-Indian Ocean connections were around the southern tip of Africa. The low temperatures of oceanic waters in high southern latitudes since the beginning of the Oligocene would seem a significant barrier to dispersal for a eucidarid. The oldest known eucidarid is *Eucidaris strobilata* from the late Eocene or early Oligocene of New Zealand; a similar form had reached southeastern Australia in the early Miocene. It is possible that larvae from early stocks of this species were dispersed westward to South Africa and northward in the Atlantic. Eocene currents south of New Zealand and Australia probably flowed in the opposite direction (Frakes and Kemp, 1972, fig. 1). However, in the absence of a strong Circum-Antarctic Current, there may have been monsoonlike changes in direction such as now occur in the Indian Ocean. Alternatively, an Eocene west wind drift from New Zealand might have been capable of carrying larvae eastward to the South Atlantic. There is, however, another possible route.

It is now known that *Eucidaris* was represented in the Caribbean as early as the middle Miocene by *E. madrugensis*, well before the Tethys connection between the Atlantic and Indian Ocean was lost. An ancestral connection through Tethys is thus possible. However, fossil records of eucidarids from the Mediterranean area, detailed here in the discussion of *E. tribuloides*, still are questionable, and there are none yet for the Indian area.

E. madrugensis could have given rise not only to *E. tribuloides* (Recent, Caribbean) but also to *E. thouarsii* and *E. thouarsii galapagensis* (Recent, eastern Pacific), because its first appearance in the Caribbean predated closure of the Panamanian isthmus. But what about the West African populations of *E. tribuloides* and *Eucidaris clavata* (Recent, found only on St. Helena and Ascension in the South Atlantic); did these eucidarids derive from an eastern Atlantic ancestor that gave rise also to *E. madrugensis* or are they better accounted for by dispersals of *E. tribuloides* larvae from Brazil via the subsurface equatorial countercurrent, as suggested by Chesher (1966, p. 210) and Pawson (1978, p. 12)? There is no answer to this in the fossil record as presently known. *E. tribuloides africana*, reported by Dartevelle from the Pleistocene of Angola, appears from the illustrations of radioles to have been a true euci-

darid. So if west-east dispersals were involved, they may have taken place during the Pleistocene.

Calocidaris. — This genus is known only from the Recent Caribbean species *Calocidaris micans* and its probable ancestor, *Calocidaris palmeri*, from upper Miocene strata of Cuba. No possibilities for origin of this lineage were found during this study.

Extinctions and Introductions

At the end of the Cretaceous, there were world-wide extinctions (Newell, 1967, 1971), but these do not seem to be reflected in the Caribbean cidaroid fauna. Of the four genera having known Cretaceous species, only the indeterminate genus apparently did not survive the period; in the other three, Eocene species are known that may be descendants of the Cretaceous species. By the end of the Eocene, five more cidaroid genera, each monospecific, had appeared.

Table 16 shows a drastic reduction in number of genera by the Oligocene, but incompleteness of the fossil record or inaccurate dating of strata may be obscuring the true picture. *Palmerius*, *Tylocidaris* and *Fellius* apparently did perish, perhaps as a result of the drop in oceanic temperatures at the end of the Eocene. However, in three of the genera there were Miocene species that could have been continuations of Caribbean lineages dating back to the Eocene or Cretaceous, and Recent species in two other genera may have had Caribbean Eocene ancestors.

During the Miocene, three genera apparently had newly arrived in the Caribbean, and there were five *Prionocidaris* species for which Caribbean antecedents are not known. Except in *Calocidaris*, there are possible Tethys ancestors for the newly introduced species, so events in the Mediterranean may have effected the increase. Even before the Messinian, environments in the area were becoming progressively less favorable for marine organisms, probably spurring an exodus to Atlantic shores of Africa or Europe and outlying islands. There adaptations to new niches and conditions may have stimulated speciation, and the chances for larvae to be caught in east-west currents to the Caribbean probably increased.

Of the nine genera present in the Caribbean during the Miocene, seven are still represented by modern Caribbean species. Pliocene-Pleistocene links are known in only one of these. This may

be due to an incomplete fossil record, but if the living species are descendants of Caribbean fossil species, why did these lineages survive while all Caribbean prionocidarids and phyllacanthids perished by the end of the Miocene or early in the Pliocene? Regressions, lowered salinities and cooling (mentioned above) all prevailed during the late Miocene and could have been lethal stresses, but these apparently were world-wide. Why would any of them be selective for the Caribbean (also South American) species in these two genera? An event that might have had a deleterious effect on marine organisms and that probably was limited to the Caribbean and the northern coast of South America was the late Miocene and early Pliocene inception of massive infusions of terrigenous debris into the Caribbean, shown by deep-sea drilling; the debris probably came from nonvolcanic Central or South American sources or was wind blown from Africa (Saunders *et al.*, 1973, p. 1103). But again, there would seem to be no reason why prionocidarids and phyllacanthids would be selectively vulnerable.

The main feature which sets these two genera apart from the other seven is their widely spaced, conjugate or subconjugate pores and massive radioles and tests. As observed in the "Evolution" section, there appears to have been a narrowing and raising of the wall between the pores in some of the lineages in other genera, from which we might conclude that there is some ecological advantage to a cidaroid in having nonconjugate pores. Yet, both *Prionocidaris* and *Phyllacanthus* are flourishing at present in the Indo-Pacific. A possible solution to this enigma is suggested below.

FAUNAL AFFINITIES

There are a number of records of Caribbean fossil cidaroids in older literature, but in only five were genera utilized other than the "catchall" *Cidaris*, *Dorocidaris* and *Leiocidaris*. In this paper, known specimens have been assigned to 18 named and six indeterminate species in 12 named genera (three new) and two indeterminate genera. The considerable diversity of this cidaroid fauna can now be appreciated. Faunal affinities can also be better understood, although more complete descriptions, photographic illustrations and revision of the generic nomenclature of many of the Tethyan cidaroids as well as more specimens of some of the Caribbean species will be needed for a more complete synthesis.

Possible allies of the Caribbean cidaroid species are named in foregoing sections. On a faunal basis, the indications are that, of the eleven named genera (other than endemic *Calocidaris*) represented in the Caribbean fossil fauna, at least five (45 per cent) or possibly as many as eight (73 per cent) have Caribbean species that show apparent affinities with Mediterranean-area fossil species; seven or eight (64 to 72 per cent) have species with affinities with fossil and Recent Indian and Pacific Ocean species; four (36 per cent) are represented by species having affinities with fossil species from the southern and eastern United States; and three (27 per cent) have species showing affinities with northeastern South American fossil species.

In these figures are found an echo of Guppy's observation (1867, p. 150) of more than 100 years ago:

The most remarkable perhaps of the results of the investigation referred to is the close alliance exhibited between the fauna of the Caribbean Miocene and that of the European beds of Malta, Bordeaux, Dax, Vienna and Piedmont and with the existing fauna of the Eastern Seas.

Many others have found affinities between American (including Caribbean) echinoid, mollusc, coral, foraminiferal and other faunas and those of European-Mediterranean and (or) Indo-Pacific areas, including Gregory (1892), Stefanini (1924), Vaughan (1921), Tortonese (1960) and Adams (1967).^{*} However, affinities of the Caribbean cidaroids have not been studied in detail previously. With the addition of new records and updating of nomenclature in this work, the considerable affinities between the Caribbean and Mediterranean and the Caribbean and Indo-Pacific cidaroids can now be better appreciated.

During these Caribbean cidaroid studies, an interesting relationship between affinities and extinctions became apparent. In five of the 11 named genera other than *Calocidaris* for which Caribbean fossil species are known, there are living Caribbean species. In each of these five, the apparent or possible affinities of the Caribbean fossil species are almost exclusively with Mediterranean fossil species,

^{*}Another pertinent article came to my attention after my paper went to press:

Mironov, A. N.

1977. *Characteristics of the present distribution of echinoid families of different geological ages* [in Russian with English summary]. *Okeanol.*, vol. 17, No. 1, pp. 153-157.

while in three of the five (*Stereocidaris*, *Histocidaris*, *Eucidaris*), the Recent Caribbean species have close counterparts in the Indo-Pacific. Five other genera (*Prophyllacanthus*, *Phyllacanthus*, *Palmerius*, *Fellius*, *Prionocidaris*) that include fossil Caribbean species having distinct affinities with Indo-Pacific species are the only ones (along with *Tylocidaris*) that either became extinct or are no longer represented in the Caribbean fauna.

This may provide a partial answer to the question: why did *Prionocidaris* and *Phyllacanthus* die out in the Caribbean and Atlantic at the end of the Miocene or early in the Pliocene while lineages of other genera apparently survived? Perhaps the Miocene Caribbean species in some of the other genera did in fact perish at the same time as the prionocidarids and phyllacanthids, but stocks of ancestors in those other genera had managed to reach some haven in the eastern Atlantic before or during the Mediterranean crisis, and the modern Caribbean species in those genera are the result of new westward dispersals.

CARIBBEAN CIDAROIDS AS STRATIGRAPHIC INDICATORS

A few of the fossil cidaroids mentioned in this paper are sufficiently characteristic and time-restricted that they are useful in determining the age of a stratum.

Typical *Prophyllacanthus leoni* radioles are very different from other cidaroid radioles studied during this work. The large size and the closely spaced, sharply peaked, and often serrate-surfaced nodules of these radioles are very distinctive. Either alone or with fragments of large tests with conjugate pores, fragments of such radioles would be excellent indicators of the Caribbean Maestrichtian.

Test fragments with distinctly conjugate pores and high, deeply crenulate primary tubercles, particularly if medial corners of the interambulacral plates are depressed into pits, and(or) fragments from distinctly flattened, serrate-edged radioles would indicate *Fellius foveatus* and, therefore, Eocene strata.

Radioles of *Palmerius roberti* would serve as markers for the late Eocene. Fragments that are nearly circular in cross section and have smooth ridges, granular grooves between the ridges, and distinctly crenulate acetabula would serve to identify this species.

Only a few radiole specimens of *Cidaris cubensis*, of late Miocene age, are known, but flattened, widened, fan-shaped tips such as are present on some of them are not known on Caribbean radioles of any other age except Recent. Fossil radiole tips of this type, therefore, would mark the late Eocene.

There are no known cidaroids that indicate the Oligocene, because known species of that age either are found also in the late Eocene or range into the Miocene.

Well-preserved radiole fragments that are slender and more or less circular in cross-section and that have a shiny surface that either is smooth or bears a few, low, smooth ridges, particularly if slightly flared tips also are present, would indicate *Calocidaris palmeri*, known only from the Caribbean middle Miocene. Prionocidarids with either grossly spinulose radioles or radioles on which the spinules are in distinct whorls are the most distinctive of the Miocene cidaroids. Unfortunately, only *Prionocidaris clevei* seems to be sharply limited in age. It is known only from Burdigalian strata, but its very small, tightly whorled radioles might be confused with small radioles of *P. cojimarensis*, which apparently lived through the Miocene, possibly into the Pliocene.

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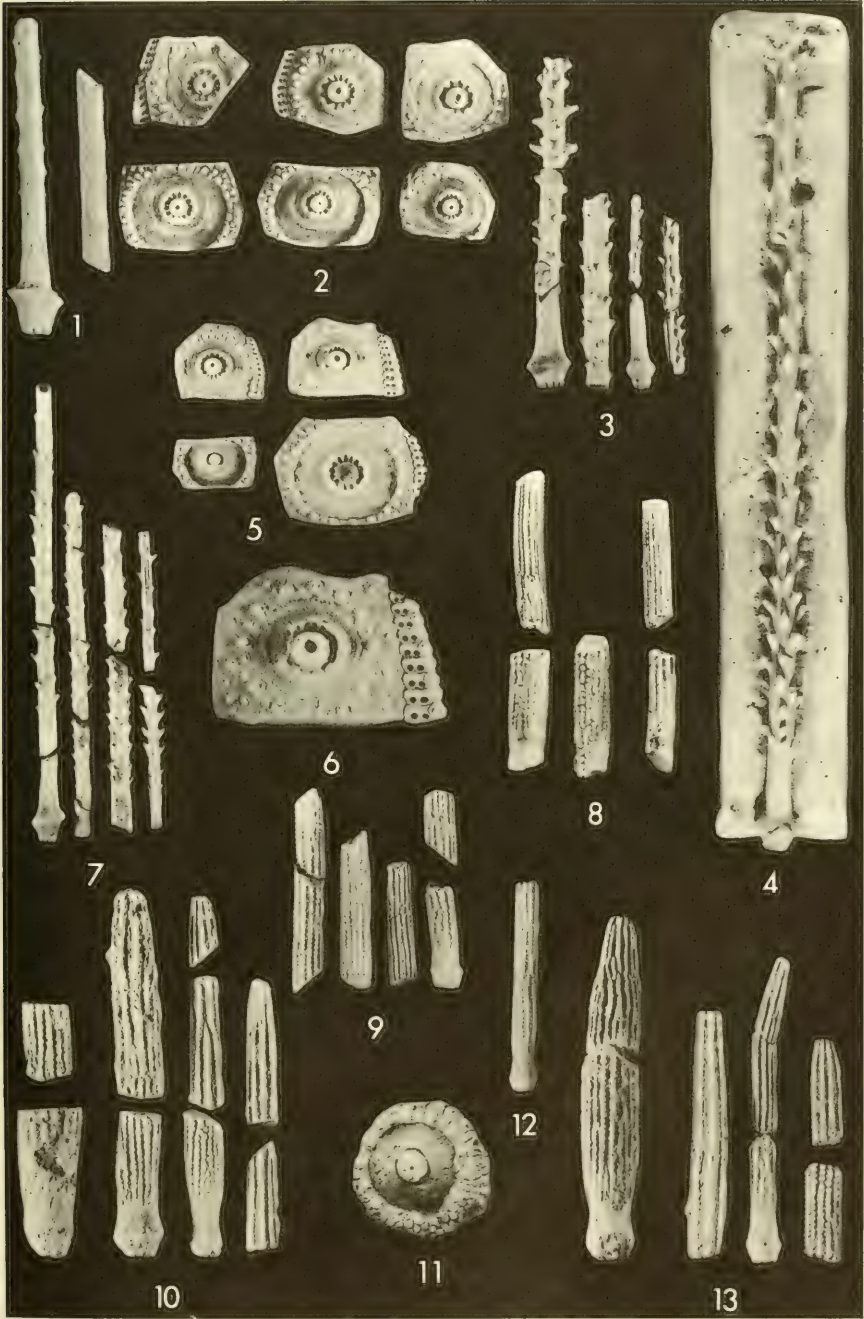
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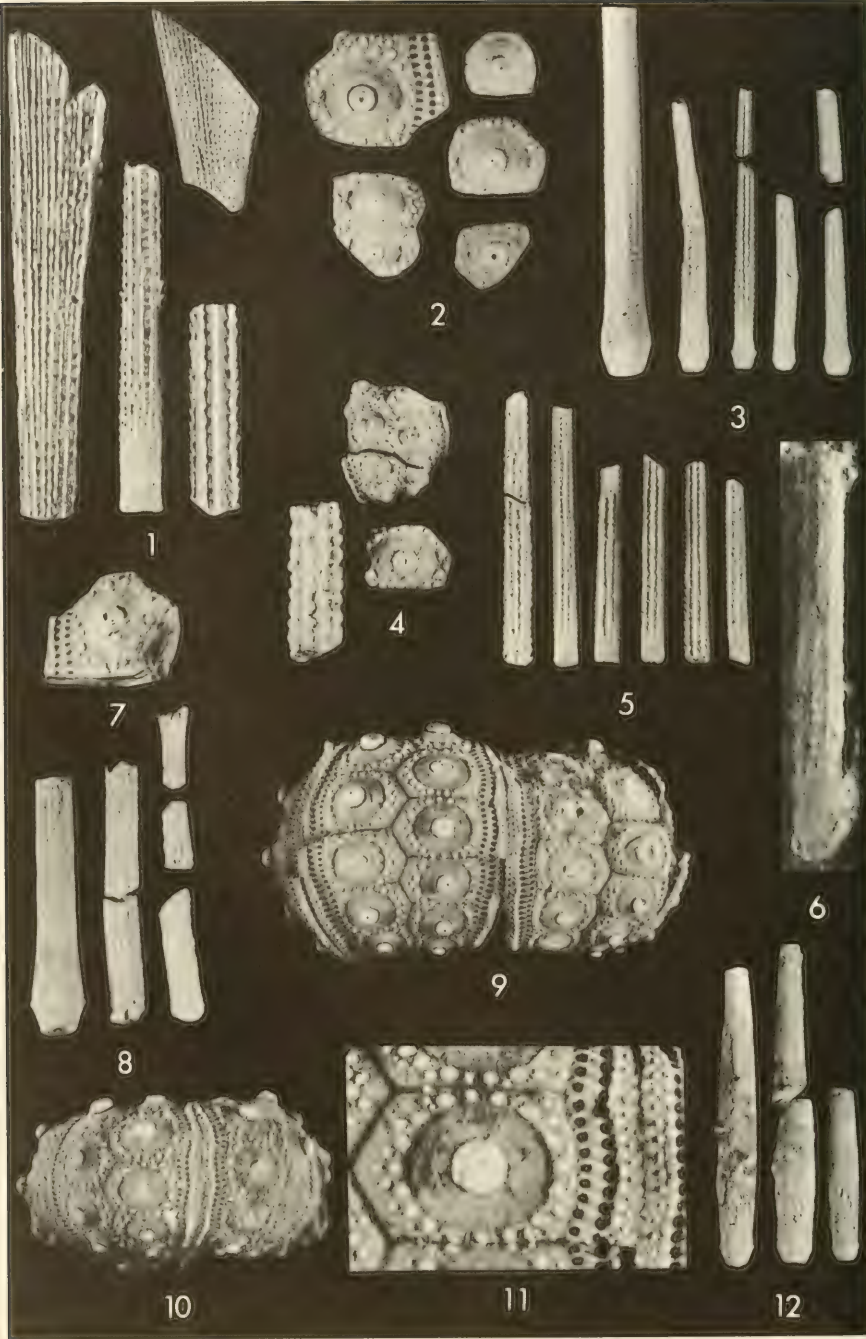
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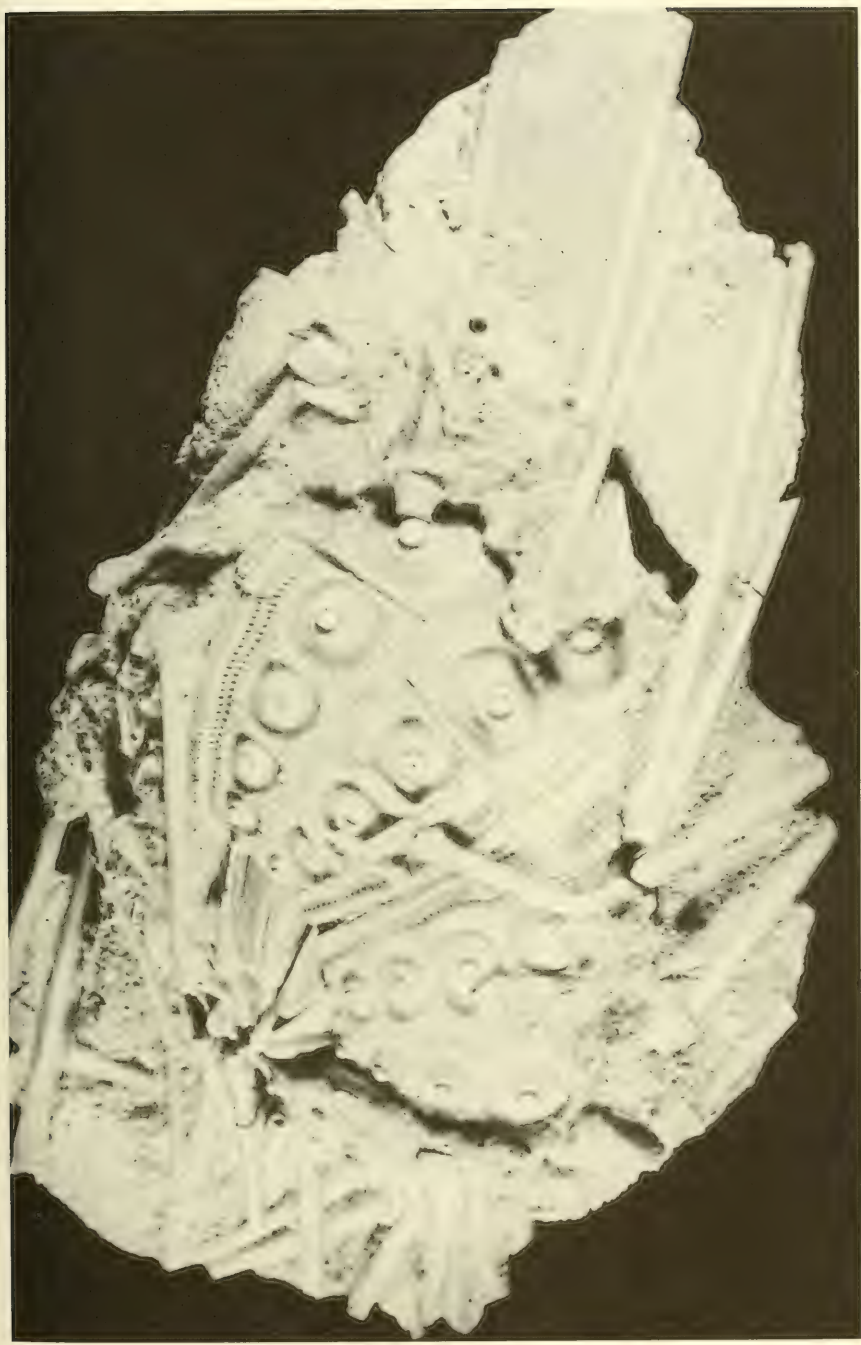


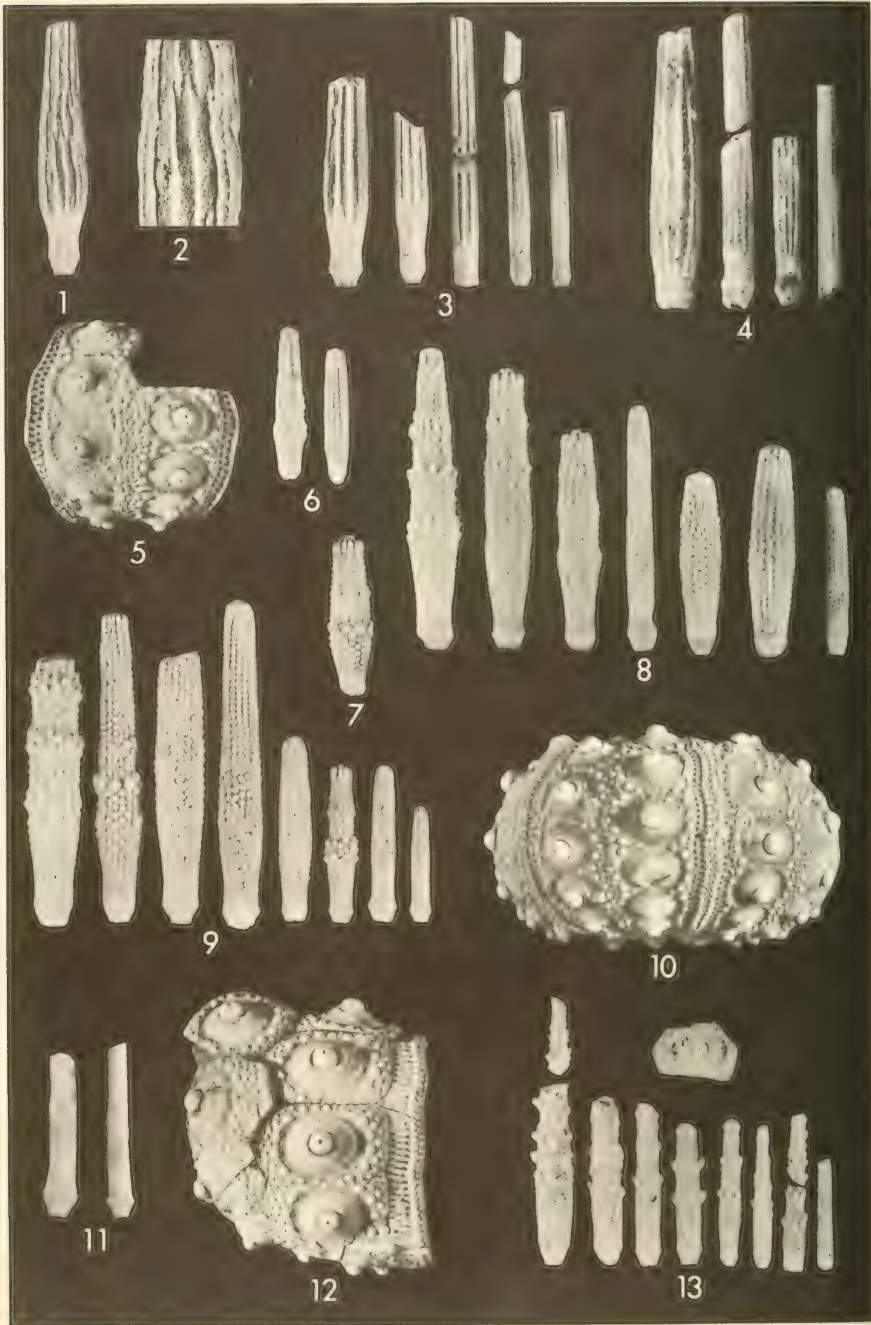
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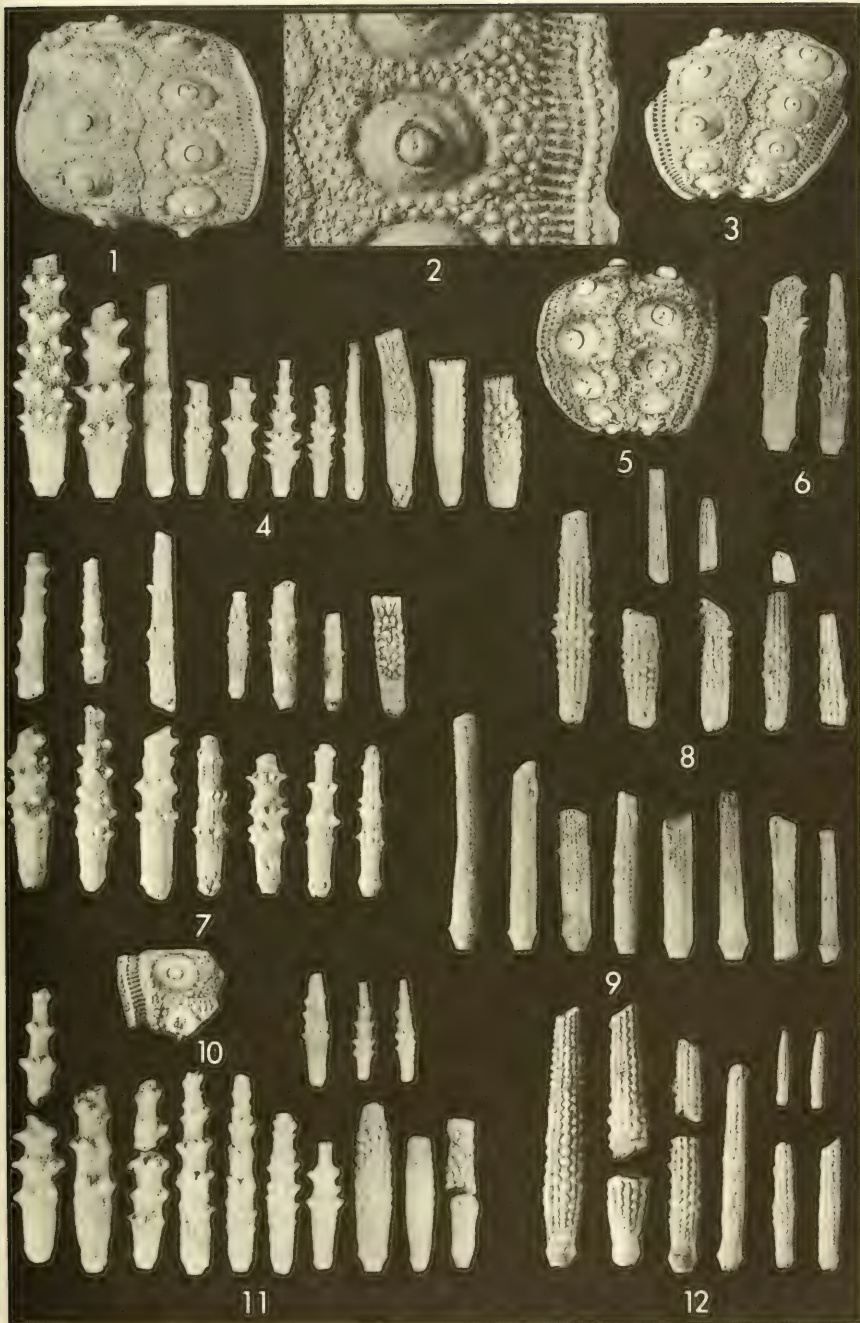


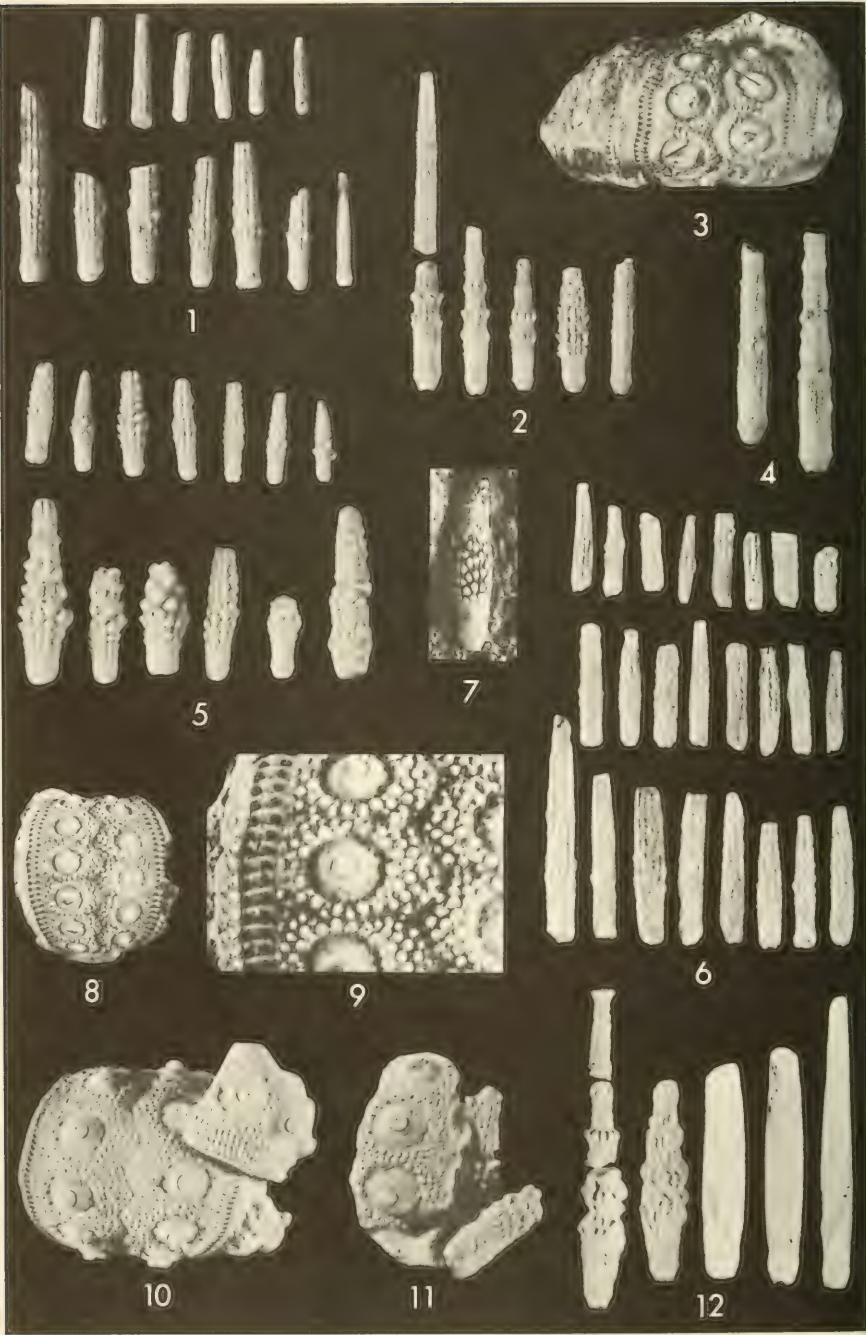
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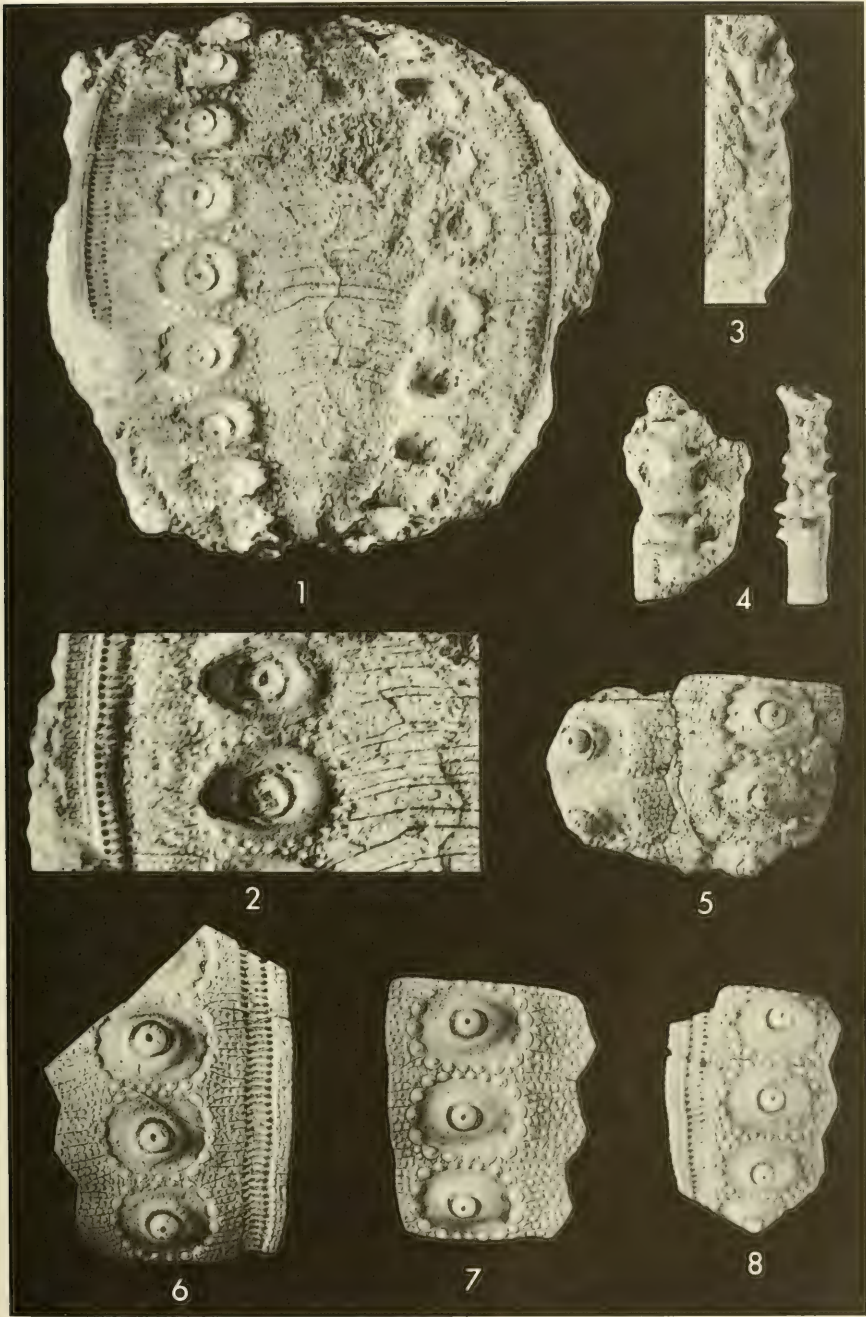


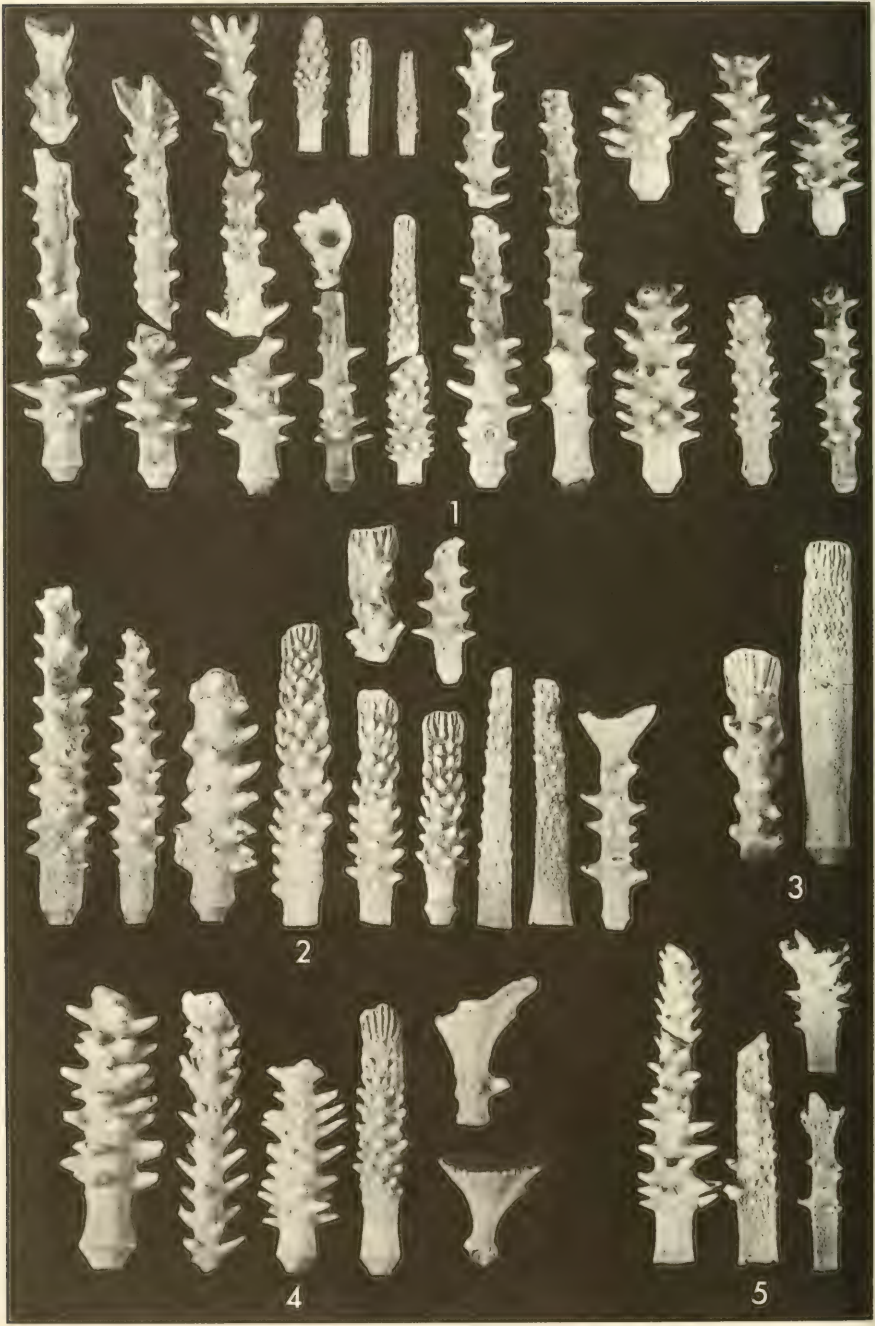
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	7. USNM 115393, radiole partially embedded in matrix, from Cleve locality (a), Anguilla, $\times 2$; 8. USNM 115400, holotype, test fragment from Cleve locality (a), Anguilla, $\times 2$; 9. portion of specimen shown in Plate 6, figure 8, $\times 6.5$; 10. BM E18256, test fragment from Earle locality (a), Anguilla, $\times 2$; 11, 12. BM E18254, BM E18257-E18259, test and radiole fragments from Earle locality (a), Anguilla, $\times 2$; all Miocene.	

EXPLANATION OF PLATE 7

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1-8.	Prionocidaris spinidentatus (Palmer in Sánchez Roig)	86
	1, 3, 4. USNM 232514, test and radiole fragments from USGS locality 44, Antigua, $\times 1$; 2. portion of specimen shown in Plate 7, figure 1, $\times 1.5$; 5. USNM 328282, test fragment from USGS locality 20, Antigua, $\times 1.5$; 6. ANSP 50977, test fragment from Palmer locality 1042, Cuba, $\times 1.5$; 7. ANSP 50980, test fragment from Palmer locality 1452, Cuba, $\times 1.5$; 8. ANSP 50982, test fragment from Palmer locality 1626, Cuba, $\times 2$; 1-5. early Miocene (Antigua Formation); 6-8. Oligocene or Miocene.	





EXPLANATION OF PLATE 8

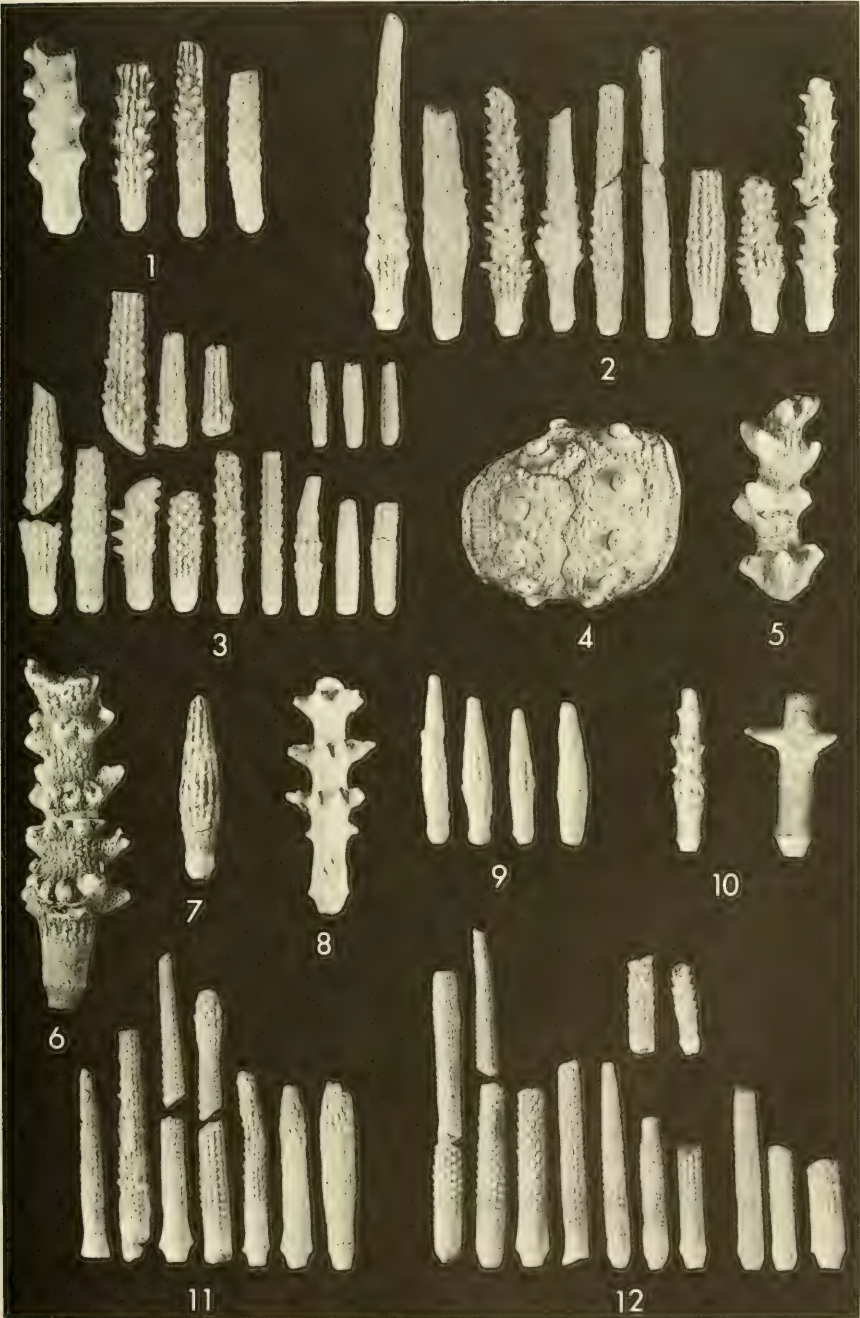
Figure

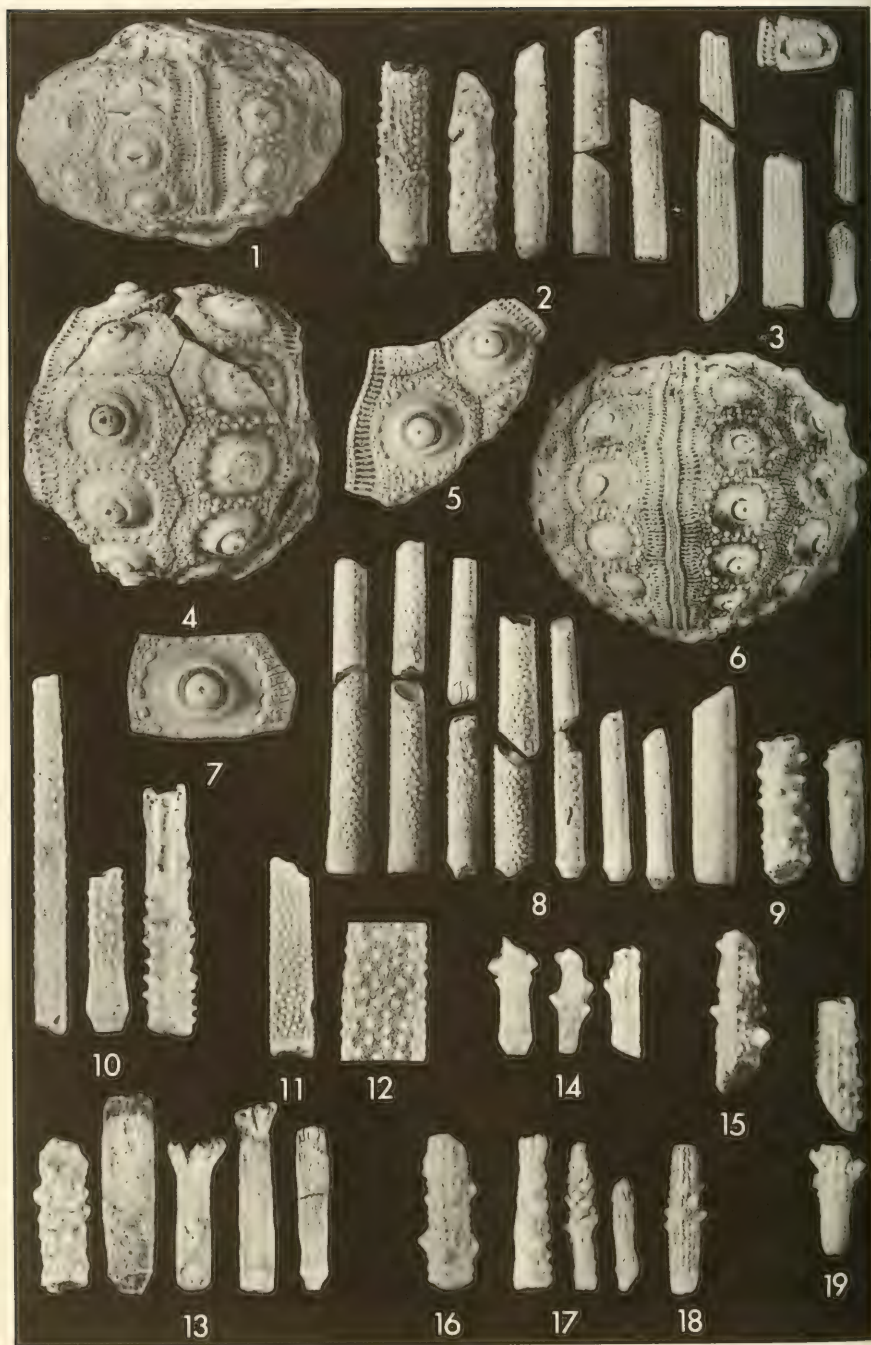
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- 1-5. **Prionocidaris spinidentatus** (Palmer in Sánchez Roig) 86
1. PRI 29682, radiole fragments from Palmer locality 1452, Cuba, $\times 1$; 2. ANSP 50978, radiole fragments and (on right) a complete, possibly adapical, radiole with cupulate tip, from Palmer locality 1042, Cuba, $\times 1$; 3. ANSP 50977, distal end of radiole and transitional radiole, from Palmer locality 1042, Cuba, $\times 1$; 4. ANSP 50981, radiole fragments from Palmer locality 1452, Cuba, $\times 1$; 5. UCMP 14428-14432, radiole fragments from UCMP locality B-3493, all Oligocene or Miocene.

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1-3.	Prionocidaris spinidentatus (Palmer in Sánchez Roig)	86
	1. PRI 29755, radiole fragments from Cutress locality 2, Puerto Rico, $\times 1$; 2, 3. PRI 29726, fragments of ridged form of radiole, from Palmer locality 1452, Cuba, $\times 1.5$; 1. Miocene (Ponce Formation); 2-3. Oligocene or Miocene.	
4-10.	Prionocidaris katherinae n. sp.	94
	4. MCZ 4102, test fragment from Palmer locality 1024, Cuba, $\times 1.5$; 5. PRI 29661, holotype, radiole fragment (in two parts) from Palmer locality 1024, Cuba, $\times 1.5$; 6. ANSP 50983, radiole from Palmer locality 1024, Cuba, $\times 1.5$; 7. PRI 29720, ridged form of radiole, from Palmer locality 1024, Cuba, $\times 2$; 8. PRI 29750, radiole fragment minus cortex, from Palmer locality 997, Cuba, $\times 1.5$; 9. PRI 29746, radioles of ridged form, from Palmer locality 997, Cuba, $\times 1.5$; 10. AMNH 18566/1,2, radiole fragments from NYAS-AMNH locality 117, Puerto Rico, $\times 1.5$; all Miocene.	
11-12.	Prionocidaris cookei Cutress	104
	11. PRI 29672, radiole fragment from Palmer locality 1034, Cuba, $\times 1.5$; 12. PRI 29670, radiole fragment from Palmer locality 601, Cuba, $\times 1.5$; all Miocene.	



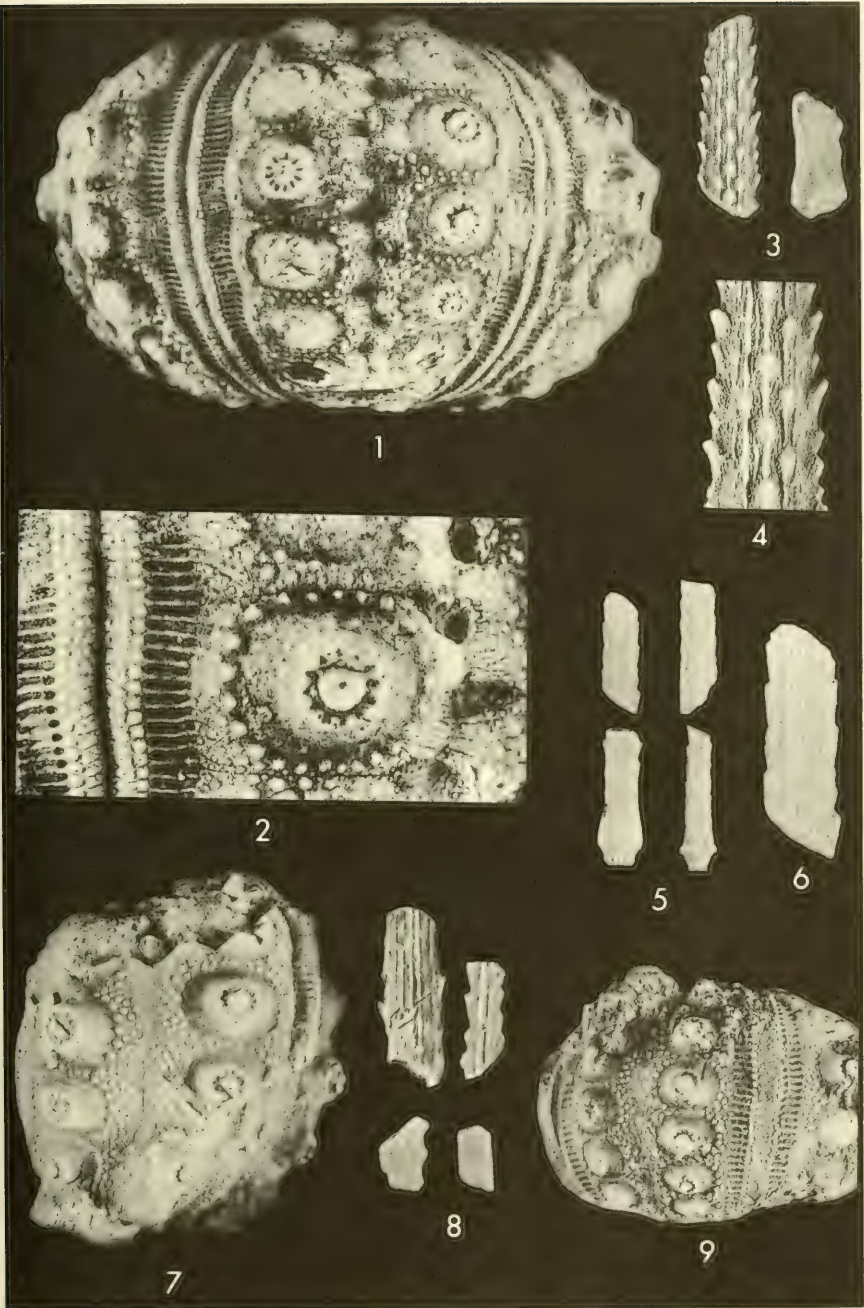


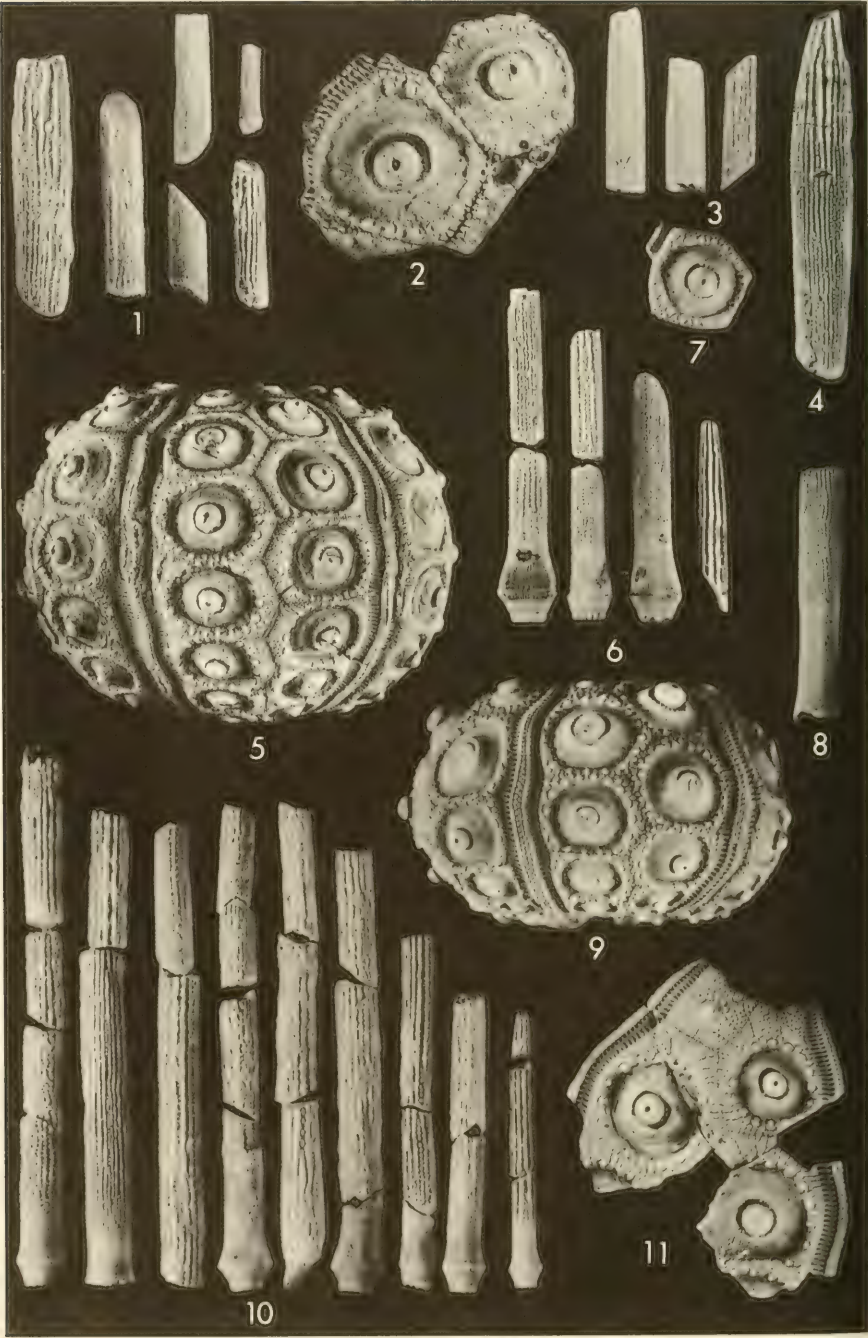
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1-19.	Prionocidaris loveni (Cotteau)	106
1.	USNM 115415, holotype, test from Cleve locality (b), St. Bartholomew, $\times 1.5$; 2. PRI 29743, radiole fragments from Palmer locality 1027, Cuba, $\times 1.5$; 3. SUPTC 10245, radiole fragments from Palmer locality 1027, Cuba, $\times 1.5$; 4. ANSP 50986, test fragment from Palmer locality D103, Cuba, $\times 1.5$; 5. ANSP 50987, test fragment from Palmer locality 591, Cuba, $\times 1.5$; 6. MCZ 4159, test from Arnold locality (b), Jamaica, $\times 1$; 7. ANSP 50979, interambulacral plate from Palmer locality 1046, Cuba, $\times 1.5$; 8. PRI 29744, fragments from typical (quincunx-patterned) radioles from Palmer locality 1046, Cuba, $\times 1$; 9. PRI 29740, radiole fragments from Palmer locality 1046, Cuba, $\times 1$; 10. SUPTC 10246, radiole fragments from Palmer locality 1640, Cuba, $\times 1.5$; 11. SUPTC 10244, radiole fragments from Palmer locality 72, Cuba, $\times 1.5$; 12. portion of radiole shown in Plate 10, figure 11, $\times 3$; 13. PRI 29679, radiole fragments, all but one fragment from nodulose form with flared tips, from Palmer locality 1090, Cuba, $\times 1.5$; 14-19. fragments from ridged form of radiole, all from Cuba, all $\times 1.5$; 14. SUPTC 10257 from Palmer locality 1003; 15. SUPTC 10258 from Palmer locality 1027; 16. PRI 29649 from Bermúdez locality 163; 17. PRI 29652 from Palmer locality 491; 18. PRI 29650 from Bermúdez locality 261; 19. CASGTC 58722 from Palmer locality 1082; locality 1090 is Oligocene, others are Eocene.	

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EXPLANATION OF PLATE 12

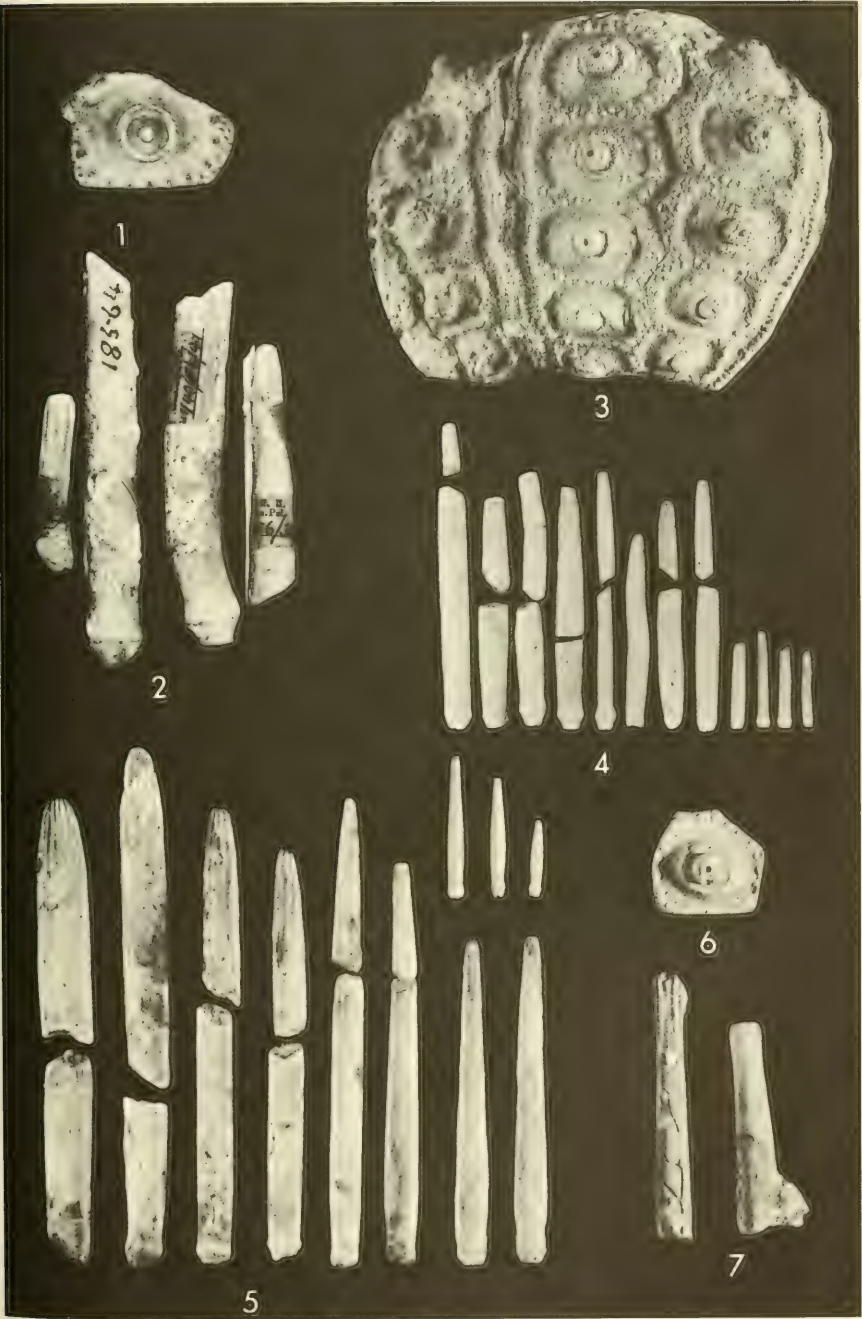
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1-4.	Prophyllacanthus eocenicus n. gen., n. sp.	127
	1. SUPTC 10250, radiole fragments from Palmer locality 1082, Cuba, $\times 1.5$; 2. SUPTC 10249a, holotype, test fragment from Palmer locality 1003, Cuba, $\times 2$; 3. SUPTC 10249b-d, radiole fragments from Palmer locality 1003, Cuba, $\times 1.5$; 4. SUPTC 10251, distal end of radiole, from Palmer locality 1085, Cuba, $\times 1.5$; all Eocene.	
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	5. UCMP 14464, test from UCMP locality B-3469, Cuba, $\times 1$; 6, 7. SUPTC 10248, radiole and test fragments from Palmer locality 1120, Cuba, $\times 1.5$; 8. PRI 29757, radiole fragment from Bermúdez locality (d), Cuba, $\times 1.5$; 9. USNM 232518, small test from USGS locality 30424, Jamaica, $\times 1.5$; 10, 11. USNM 232517, test and radiole fragments from USGS locality 29544, Jamaica, radioles $\times 1$, test $\times 1.5$; all Cretaceous.	

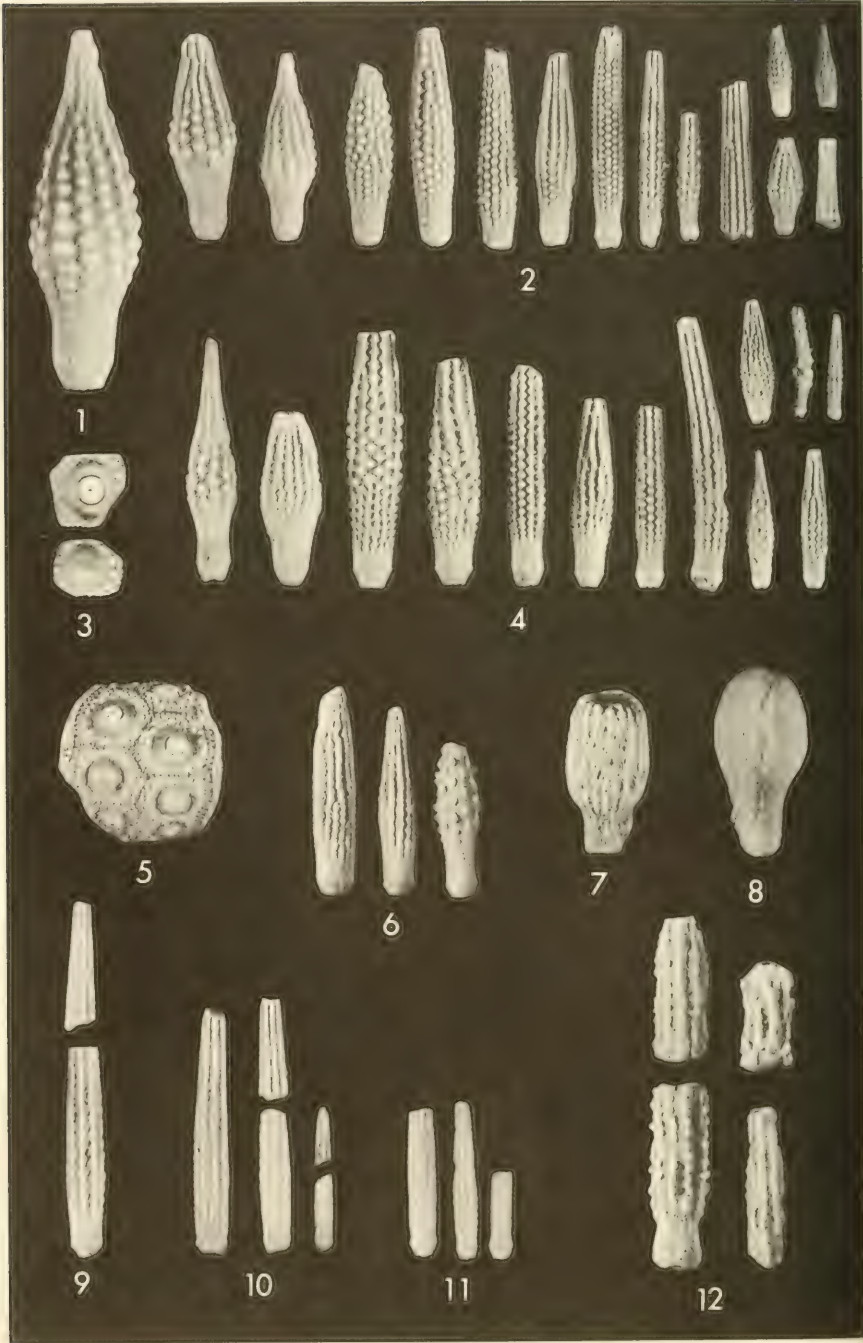
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| 1-7. | Phyllacanthus peloria (Jackson) | | 131 |
| 1. | AMNH 18564/3, holotype, interambulacral plate, from NYAS-AMNH locality 56, Puerto Rico, $\times 1.5$; | | |
| 2. | AMNH 18564/4,2,5, hypotypes, radiole fragments from NYAS-AMNH locality 56, Puerto Rico, $\times 1$; | | |
| 3. | BM E75629, test fragment from Martin-Kaye locality GR222699, Antigua, $\times 1.5$; | | |
| 4. | PRI 29645, radiole fragments from Palmer locality 1452, Cuba, $\times 1$; | | |
| 5. | PRI 29644, radiole fragments from Palmer locality 1262, Cuba, $\times 1$; | | |
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1-4.	Tylocidaris bermudezi n. sp.	134
	1. SUPTC 10252a, holotype, radiole from Palmer locality 1102, Cuba, $\times 4$; 2, 3. SUPTC 10252b-r, radioles and test fragments from Palmer locality 1102, Cuba, $\times 2$; 4. SUPTC 10253, radioles from Palmer locality 1640, Cuba, $\times 2$; all Eocene.	
5-8.	Tylocidaris sp. A	137
	5. UCMP 14502, test fragment from UCMP locality B-3290 (= Palmer loc. 757), Cuba, $\times 2$; 6. SUPTC 10254, radiole from Palmer locality 757, Cuba, $\times 2$; 7. SUPTC 10256, radiole from Palmer locality 832, Cuba, $\times 2$; 8. PRI 29712, radiole from Palmer locality 812, Cuba, $\times 2$; all Cretaceous.	
9-11.	Indeterminate genus A	140
	9. PRI 29736, radiole fragments from Palmer locality 1393, Cuba, $\times 1.5$; 10. PRI 29737, radiole fragments from Palmer locality 1593, $\times 1.5$; 11. PRI 29666, radiole fragments from Palmer locality 299, Cuba, $\times 1.5$; all Miocene.	
12.	Indeterminate genus B	141
	12. USNM 243089, radiole fragments from USGS locality 30066, Jamaica, $\times 2$; Cretaceous.	

APPENDIX

Measurements of selected test characters in some Recent Cidaroida

Species	No. Spec. (mm)	Test HD	Test	Aspd/HD (%)	Perd/HD (%)	Range Mean	Range Mean	VD/HD (%)	Aspd/Lanasp (%)	Aspd/Lanasp (%)	Act/Lanasp (%)	Range Mean	Range Mean	MM/Lanasp (%)	Range Mean	APL: Lanasp (No.)	APL: Lanasp (No.)	APL: Lanasp (No.)	APL: Lanasp (No.)
<i>Calcidiscus</i>	4	70-78	34-37	36	35-37	37	83-86	84	18-24	21	55-58	56	26-33	29	16-17	9-11	10-1	10-1	10-1
"	4	52-60	40-47	42	38-42	40	67-83	70	17-23	21	53-63	58	23-27	26	14-15	7-9	8-8	8-8	8-8
"	2	43-48	44-51	48	44	44	61-79	70	25-28	27	57-65	61	22-29	26	10	6	6	6	6
"	1	34	47	47	47	47	71	71	24	24	60	60	25	25	13	6	6	6	6
<i>Chondrocidaris</i>	3	82-85	35-37	36	37-38	38	59-62	61	19-22	21	48-49	49	32-36	36	15-16	8-9	8-9	8-9	8-9
"	3	74-77	38-44	40	39-45	41	60-68	64	18-21	20	49-58	55	32-39	33	15-16	7-9	7-9	7-9	7-9
<i>Cidar</i>	2	65-70	56-57	57	57	57	64-66	65	19-21	20	50-53	52	25-29	27	12	7-8	7-8	7-8	7-8
"	5	34-59	41-49	44	34-38	36	62-80	70	20-34	24	58-53	59	23-28	26	12-17	7-8	7-8	7-8	7-8
"	16	51-55	45-53	49	45-53	49	54-64	59	20-27	24	60-68	64	18-25	23	9-13	5-6	5-6	5-6	5-6
"	6	21-28	44-55	48	40-54	48	52-63	58	21-25	24	60-75	66	16-27	23	11-13	5-6	5-6	5-6	5-6
"	6	15-20	50-57	52	45-53	48	50-66	57	20-27	25	61-70	67	20-25	22	9-12	5-6	5-6	5-6	5-6
"	2	9-10	56-70	63	55-56	56	55-56	56	24-28	26	60-67	64	23-30	26	7	4-5	4-5	4-5	4-5
<i>Blakel (A. Agassiz)</i>	5	42-46	39-48	44	33-43	37	58-70	65	21-26	24	61-69	65	19-26	22	13	7-8	7-8	7-8	7-8
"	6	22-30	42-55	47	37-40	37	58-70	65	21-26	24	61-69	65	19-26	22	13	7-8	7-8	7-8	7-8
"	6	22-30	45-56	50	37-40	38	55-67	61	18-26	21	64-75	67	17-20	18	11-12	6-7	6-7	6-7	6-7
"	7	13-18	46-51	41	41-54	44	53-62	57	22-33	26	57-75	67	19-29	23	8-10	5-7	5-7	5-7	5-7
"	3	8-9	56-63	58	50-56	52	50-56	52	25-37	33	67-75	69	17-22	20	6-7	4-5	4-5	4-5	4-5
<i>Cidar</i>	1	49	45	45	39	39	63	63	33	33	66	66	22	22	12	7-8	7-8	7-8	7-8
"	5	24-28	42-51	46	40-44	43	57-61	59	22-23	22	67-73	69	13-20	17	8-11	6-7	6-7	6-7	6-7
<i>Eugenia (H. L. Clark)</i>	12	31-40	40-49	46	35-48	42	55-68	62	19-29	26	58-71	65	19-26	23	11-13	6-8	6-8	6-8	6-8
"	10	24-28	47-53	49	38-47	44	59-64	62	24-27	25	68-75	71	18-22	20	7-9	5-7	5-7	5-7	5-7
"	4	14-19	47-53	51	42-51	47	54-61	57	24-27	25	68-75	71	18-22	20	7-9	5-7	5-7	5-7	5-7
<i>Eucidaris</i>	3	51-56	31-40	35	41-43	42	60-61	60	17-24	21	58-70	63	18-29	26	13-14	8-10	8-10	8-10	8-10
"	2	45-50	34-38	36	43-47	45	56-66	61	21-23	22	70-71	71	19-21	20	13-14	7-9	7-9	7-9	7-9
"	5	35-40	41-53	36	39-49	43	54-61	59	21-28	24	58-71	65	19-26	23	11-13	6-8	6-8	6-8	6-8
"	5	23-27	37-46	42	38-45	43	50-59	54	25-30	28	58-71	65	19-26	23	11-13	6-8	6-8	6-8	6-8
"	11	11-16	42-50	46	42-50	46	42-50	46	25-30	28	58-71	65	19-26	23	11-13	6-8	6-8	6-8	6-8
"	12	6-10	42-68	52	37-53	48	38-50	44	20-34	30	58-75	69	17-29	21	5-6	5-6	5-6	5-6	5-6
<i>tribuloides (Lamarck)</i>	5	41-50	32-42	38	31-38	35	54-62	58	21-30	25	46-52	48	32-42	38	10-11	9-10	9-10	9-10	9-10
"	5	41-50	36-54	43	34-45	42	48-56	53	20-31	24	48-53	54	23-38	33	9-10	7-9	7-9	7-9	7-9
"	5	23-27	37-46	42	38-45	43	50-59	54	25-30	28	58-71	65	19-26	23	11-13	6-8	6-8	6-8	6-8
"	11	11-16	42-50	46	42-50	46	42-50	46	25-30	28	58-71	65	19-26	23	11-13	6-8	6-8	6-8	6-8
"	12	6-10	42-68	52	37-53	48	38-50	44	20-34	30	58-75	69	17-29	21	5-6	5-6	5-6	5-6	5-6
<i>Heterocidar</i>	1	53	42	42	38	38	70	70	24	24	73	73	17	17	11	9-10	9-10	9-10	9-10
"	2	31-38	49-50	48	35-39	37	58-63	61	20-28	24	65-70	67	20-24	24	8-10	7-8	7-8	7-8	7-8
<i>shagerei (A. Agassiz)</i>	2	82-85	46-52	49	36-46	39	70-72	71	21-23	22	56-57	57	23-26	26	13-14	9-11	9-11	9-11	9-11
"	4	62-67	40-45	42	32-37	32	66-81	73	17-22	22	63-68	65	21-25	23	11-12	8-9	8-9	8-9	8-9
<i>Phylacanthus</i>	1	73	33	33	47	47	62	62	20	20	65	65	20	20	18	7	7	7	7
"	4	61-69	32-44	31	35-41	37	62-64	61	19-21	20	65-70	67	20-24	24	8-10	7-8	7-8	7-8	7-8
"	4	61-69	32-44	31	35-41	37	62-64	61	19-21	20	65-70	67	20-24	24	8-10	7-8	7-8	7-8	7-8
"	5	42-48	27-38	34	38-52	48	48-64	57	16-19	18	70-83	76	13-25	17	13-17	5-7	5-7	5-7	5-7
"	5	30-39	30-43	36	42-50	46	53-60	57	18-26	21	72-80	71	13-25	18	13-17	5-7	5-7	5-7	5-7
<i>Pleurocidaris</i>	1	83	41	41	33	33	60	60	22	22	54	54	28	28	16	9-10	9-10	9-10	9-10
"	2	75-80	36-39	38	30-37	34	55-61	58	30-31	31	50-54	52	29-32	31	14-16	9-10	9-10	9-10	9-10
"	22	41-50	37-46	41	33-60	39	46-61	59	25-31	27	57-66	61	21-27	24	11-13	7-9	7-9	7-9	7-9
"	20	21-40	38-46	42	34-42	39	43-68	56	22-32	26	60-72	66	18-25	22	8-10	6-8	6-8	6-8	6-8
"	10	22-30	39-48	43	39-42	40	44-80	55	24-30	27	67-75	71	18-20	19	8-10	6-8	6-8	6-8	6-8
"	6	12-20	43-48	45	41-48	45	45-52	50	25-31	27	70-79	73	15-21	19	8-10	6-8	6-8	6-8	6-8
<i>biapinosa (Lamarck)</i>	1	43	44	44	46	46	61	61	23	23	67	67	21	21	12	12	12	12	12
"	4	31-35	44-48	46	44-46	45	54-60	57	20-24	22	68-72	70	20-28	25	11-13	7-9	7-9	7-9	7-9
"	2	25-30	27-43	35	27-45	36	26-60	43	21-20	26	72-78	75	13-21	19	8-10	6-8	6-8	6-8	6-8
"	4	12-18	43-52	46	46-54	49	47-53	50	23-27	25	70-75	71	18-20	19	8-10	6-8	6-8	6-8	6-8
"	7	6-10	47-64	53	42-64	49	43-56	48	28-44	32	70-75	71	18-20	19	8-10	6-8	6-8	6-8	6-8
<i>verticillata (Lamarck)</i>	5	31-37	43-49	46	41-52	46	48-55	52	31-36	33	56-59	58	26-32	29	10-14	9-10	9-10	9-10	9-10
"	7	22-29	43-50	48	43-52	48	48-52	51	22-40	33	64-72	68	17-27	21	9-11	8-9	8-9	8-9	8-9
"	6	12-20	48-56	52	43-58	51	43-50	50	33-41	37	67-71	69	20-25	22	6-7	4-5	4-5	4-5	4-5
"	2	9-10	50-56	53	45-56	51	45-50	50	33-41	37	67-71	69	20-25	22	6-7	4-5	4-5	4-5	4-5
<i>Stereocidar</i>	1	22	47	47	37	37	65	65	30	30	67	67	25	25	7	6	6	6	6
"	9	23-30	49-54	52	43-52	49	50-56	53	26-30	28	60-67	62	23-31	26	10-13	7-9	7-9	7-9	7-9
"	2	11-20	51-59	55	44-50	47	50-51	51	25-29	27	67-75	71	16-22	19	9-10	7-8	7-8	7-8	7-8
<i>Stylocidar</i>	12	21-32	43-50	45	40-48	44	52-63	48	26-35	28	58-75	68	17-20	24	12-15	5-6	5-6	5-6	5-6
"	8	15-20	47-60	55	42-50	45	47-57	52	25-33	28	60-78	68	18-27	24	9-13	5-6	5-6	5-6	5-6
<i>Trochocidar</i>	1	63	43	43	40	40	66	66	22	22	52	52	27	27	15	14	14	14	14
"	5	52-56	40-53	41	37-41	39	59-65	61	19-26	21	51-54	57	18-27	26	13-15	8-9	8-9	8-9	8-9
"	4	48-50	38-45	43	36-42	39	55-63	59	21-25	24	52-60	56	24-27	23	11-13	7-8	7-8	7-8	7-8
"	7	31-40	43-51	46	38-46	42	53-64	58	20-29	25	49-59	59	22-32	27	12-16	7-8	7-8	7-8	7-8
"	4	23-28	35-50	44	41-45	43	57-53	53	23-28	25	50-53	53	23-27	26	11-14	7-8	7-8	7-8	7-8
"	1	15	47	47	47	47	53	53	25	25	56	56	22	22	11	11	11	11	11

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